THE QUARTERLY REVIEW OF BIOLOGY

JUNE
1957

Vol. 32 No. 2

Published by
THE AMERICAN INSTITUTE
OF BIOLOGICAL SCIENCES

Copyright 1957
The American Institute of
Biological Sciences

THE QUARTERLY REVIEW OF BIOLOGY

FOUNDED BY RAYMOND PEARL

B. H. WILLIER, *Editor*
The Johns Hopkins University

H BENTLEY GLASS
Associate Editor

CARL P. SWANSON
Assistant Editor

Editorial Office:
Department of Biology, The Johns Hopkins University,
Baltimore 18, Maryland

Advisory Board

IRVING W. BAILEY ..... *Harvard University*
G. W. BEADLE ..... *California Institute of Technology*
DAVID R. GODDARD ..... *University of Pennsylvania*
ROSS G. HARRISON ..... *Yale University*
LIBBIE H. HYMAN ..... *American Museum of Natural History*
A. L. KROEBER ..... *University of California*
K. S. LASHLEY ..... *Harvard University*
DANIEL MAZIA ..... *University of California*
CHARLES W. METZ ..... *University of Pennsylvania*
THOMAS PARK ..... *University of Chicago*
ALFRED S. ROMER ..... *Harvard University*
ALEX G. RUTHVEN ..... *University of Michigan*
F. O. SCHMITT ..... *Massachusetts Institute of Technology*
PAUL WEISS ..... *Rockefeller Institute*

Papers to Appear in an Early Number

QUANTITATIVE LAWS IN METABOLISM AND GROWTH
Ludwig von Bertalanffy, *Mt. Sinai Hospital and University of Southern California*

A THEORY OF THE CONTROL OF DIFFERENTIATION IN THE CELLULAR SLIME MOLDS
John Tyler Bonner, *Princeton University*

CENTRIFUGAL SPECIATION
William L. Brown, Jr., *Museum of Comparative Zoology*

Entered as second-class matter January 27, 1926, at the Post Office at Baltimore, Maryland, under the act of March 3, 1879. Published quarterly at Mt. Royal and Guilford Aves., Baltimore 2, Md., by The American Institute of Biological Sciences, Business Office, 2000 P Street, N.W., Washington 6, D.C. Subscription price, $7.50 a year ($6.50 to members of A.I.B.S.; $8.25 outside U.S.A., except Canada, Canada, $7.75). $2.00 a single copy, when available, $.25 postage outside U.S.A.

Made in United States of America

Annals of Human Genetics

(FORMERLY ANNALS OF EUGENICS)

Edited by L. S. PENROSE *with the assistance of*
JULIA BELL, R. A. FISHER, J. B. S. HALDANE, MARY N. KARN, R. R. RACE, J. A. F. ROBERTS AND C. A. B. SMITH

Contents of Vol. XXI. Part 4. June 1957

Familial distribution of erythrocyte sedimentation rate. M. FRACCARO
Body size and weight in relation to varicocoele and hernia. SHEILA M. SMITH
Defective colour vision, PTC tasting and drepanocytosis in samples from fifteenth Brazilian populations. H. KALMUS
Dystrophia myotonica with special reference to Northern Ireland. MARGARET A. LYNAS
Genetics of dermal ridges. Sib pair correlations for total finger ridge-count. SARAH B. HOLT
Note on the estimation of intraclass correlation. C. A. B. SMITH
Le nombre de dermatoglyphes dans un echantillon de jumeaux. M. LAMY, J. FREZAL, J. DE GROUCHY ET MME J. KELLEY
The Log-likelihood ratio test (the G-test). Methods and table for test of heterogeneity in contingency tables. B. WOOLF
Further families showing linkage between the *ABO* and nail-patella loci with no evidence of heterogeneity. SYLVIA D. LAWLER, J. H. RENWICK AND L. S. WILDERVANCK
Blood groups and haemoglobin variants in Nigerian (Yoruba) school children. N. A. BARNICOT AND J. P. GARLICK
Reviews Ageing in transient tissues. *Edited by* G. E. W. WOLSTEN-HOLME AND E. C. P. MILLAR, R. BILLINGHAM
Biology of the laboratory mouse. *Edited by* G. D. SNELL, A. G. SEARLE

Subscription price $13.50 net per volume.
Single issues $4.50 plus postage.

Issued by the **CAMBRIDGE UNIVERSITY PRESS**

32 East 57th Street, New York 22, N. Y.

ECOLOGY

Official Publication of the ECOLOGICAL SOCIETY OF AMERICA

Continuing the Plant World

Editors:

Edward S. Deevey (Zoology), Yale University **Alton A. Lindsey (Botany), Purdue University**

Vol. 38, No. 4 Table of Contents October, 1957

Availability of iron and manganese in southern Wisconsin lakes for the growth of *Microcystis aeruginosa* GERALD C. GERLOFF AND FOLKE SKOOG
Nitrogen as a limiting factor for the growth of *Microcystis aeruginosa* in southern Wisconsin lakes GERALD C. GERLOFF AND FOLKE SKOOG
Altitudinal distribution of some Entomostraca in Colorado ..... EDWARD B. REED AND JOHN R. OLIVE
Factors influencing variations in populations of *Anopheles quadrimaculatus* in southwestern Georgia MELVIN H. GOODWIN, JR. AND G. J. LOVE
Lethal effects of high temperatures on the immature stages of *Anopheles quadrimaculatus* ..... G. J. LOVE AND J. G. WHELCHE
Life history of *Australorbis glabratus*, the intermediate snail host of *Schistosoma mansoni* in Puerto Rico ..... DAVID PIMENTEL
Further notes on the population ecology of the spadefoot toad ..... PAUL G. PEARSON
Determination and analysis of recurrent groups ..... EDWARD W. FAGER
The effects of light and temperature on the fecundity of the greenthroat darter, *Etheostoma lepidum* Girard CLARK HUBBS AND KIRK STRAWN
Fir-Spruce-Birch forest in northern Minnesota ..... MURRAY F. BUELL AND WILLIAM A. NIERING
Some sampling characteristics of a series of aggregated populations GRANT COTTAM, J. T. CURTIS, AND ANTHONY J. CATANA, JR.
Phenological observations of nineteen native tree species ..... CLIFFORD E. AHLGREN
Soil microfungi in relation to the prairie continuum in Wisconsin ..... P. A. ORPURT AND J. T. CURTIS
A phytosociological ordination of the conifer swamps of Wisconsin ..... J. JOHANNA CLAUSEN
Some silvicultural characteristics of western redcedar in southeast Alaska ..... R. A. GREGORY

NOTES AND COMMENT

Current Subscription, in the United States, Canada, and the Pan-American countries, $7.50 a year for complete volumes; other foreign countries—$.60 a year additional for postage;
Single Issue, $2.00; Back Volumes, as available, $8.00.
Orders should be placed with

DUKE UNIVERSITY PRESS

College Station, Box 6697 Durham, North Carolina

(In writing to advertisers, please mention the journal—it helps.)

IN BIOLOGY

NEARLY

EVERYBODY

READS

THE

AIBS BULLETIN

Russian Translations in Biology

PROCEEDINGS OF THE ACADEMY OF SCIENCES OF THE USSR (DOKLADY)

BIOLOGICAL SCIENCES SECTION

Subscription Rates, 6 issues per year, $20.00 per year U. S. & Can., $22.00 per year Foreign
Single Copies $4.00

BOTANICAL SCIENCES SECTION

Subscription Rates, 6 issues per year, $7.50 per year U. S. & Can., $9.00 per year Foreign
Single Copies $1.50

MICROBIOLOGY

Subscription Rates, 6 issues per year, $20.00 per year U. S. & Can., $22.50 per year Foreign
Single Copies $4.00

PLANT PHYSIOLOGY

Subscription Rates, 6 issues per year, $15.00 per year U. S. & Can., $17.00 per year Foreign
Single Copies $3.00

Each journal will appear in translation approximately 3 to 4 months after publication in Russian. The English translations will bear the Russian volume and issue numbers. All subscriptions will be on a calendar year basis.

Applications for subscriptions and all inquiries should be directed to:

AMERICAN INSTITUTE OF BIOLOGICAL SCIENCES
2000 P St., N.W. Washington 6, D. C.

(In writing to advertisers, please mention the journal—it helps.)

A.I.B.S.
Symposium Proceedings Series

By early fall three volumes in this new series will be available. Each contains complete proceedings, including discussions, of symposia sponsored by the Office of Naval Research and published by A.I.B.S.

Molecular Structure and Functional Activity of Nerve Cells

Edited by R. G. GRENELL *and* L. J. MULLINS

Chemoreceptor Mechanisms, V. G. Dethier; Visual Receptors as Biological Transducers, E. F. MacNichol, Jr.; Affinity for Wool as an Indicator of Neuropharmacological Activity, R. Fischer; Oxygen Utilization in Sympathetic Ganglia, M. G. Larrabee and P. Horowitz; The Structure of Nerve Cell Membranes, L. J. Mullins. Discussants: W. D. McElroy, P. W. Davies, and R. G. Grenell.

Appeared January 1957. $4.75 ($3.75 to AIBS Members)

Molecular Structure and Biological Specificity

Edited by LINUS PAULING *and* H. A. ITANO

Molecular Complementariness in Antigen-Antibody Systems, D. Pressman; Nature and Formation of Antibodies, F. Haurowitz; Specific Attraction Between Identical Macromolecules, H. Jehle; Hydrogen Binding, J. Donohue; Intermolecular Forces, J. O. Hirschfelder; Interaction of Organic Molecules with Proteins, I. M. Klotz; The Effect of Dye Structure on Affinity for Fibers, H. E. Schroeder and S. N. Boyd; On the Structural Basis of Ribonuclease Activity, C. B. Anfinsen and R. R. Redfield; Molecular Shapes, Especially Orientation around Single Bonds, K. S. Pitzer; Specificity and Inhibition of Fumarse, R. A. Alberty; Specificity in the Interaction of Sickle Cell Hemoglobin Molecules. H. A. Itano; Specificity in Cholinesterase Reactions, I. B. Wilson.

Ready in September 1957. $4.75 ($3.75 to AIBS Members)

Ultrasound in Biology and Medicine

Edited by E. KELLY

Acoustic Properties of Blood and its Components, E. L. Carstensen and H. P. Schwan; Physical Aspects of High Amplitude Sound Phenomena, W. L. Nyborg; Progress in the Techniques of Soft Tissue Examination by 15MC Pulsed Ultrasound, J. J. Wild and J. M. Reid; Techniques Used in Ultrasonic Visualization of Soft Tissues, D. H. Howry; The Indications and Contra-indications for Ultrasonic Therapy in Medicine, J. H. Aldes; Neurosonic-surgery, W. J. Fry and F. J. Fry; Histological Study of Changes Produced by Ultrasound in the Gray and White Matter of the Central Nervous System, J. W. Barnard, J. F. Brennan and W. J. Fry; On the Problem of Dosage in Ultrasonic Lesion Making, H. T. Ballantine, Jr., W. C. Cotter and T. F. Hueter; Some Examples of Ultrasonic Frequency Sensitive and Frequency Insensitive Biological Reactions, Rene-Guy Busnel; A Forum on an Ultrasonic Method for Measuring the Velocity of Blood, E. J. Baldes, W. R. Farrall, M. C. Haugen and J. F. Herrick; Destructive Effects of High-intensity Ultra-sound on Plant Tissues, J. F. Lehmann, E. J. Baldes and F. H. Krusen; Generating and Measuring High-intensity Ultrasound of Frequencies Between 1 and 68 Megacycles, B. B. Check; Some Changes in Liver Tissue which Survives Irradiation with Ultrasound, E. Bell; An Ultrasonic Dosage Study; Functional Endpoint, F. Dunn and W. J. Fry; Thermocouple Probes, W. J. Fry.

Ready in September 1957. $4.75 ($3.75 to AIBS Members)

Orders and all inquiries should be directed to:

AMERICAN INSTITUTE OF BIOLOGICAL SCIENCES

2000 P St., N.W. Washington 6, D. C.

(In writing to advertisers, please mention the journal—it helps.)

AMERICAN INSTITUTE OF BIOLOGICAL SCIENCES PLACEMENT SERVICE

Do you have staff vacancies for biologists?

So that you may become acquainted with the activities of this Service, we will be pleased to send a complimentary copy of the June List of Registrants.

This Directory contains resumes of 101 highly specialized biologists.

To employers of biologists the AIBS offers a three-fold Placement Service:

1. A list of available biologists with a summary of the qualifications of each published in booklet form in June and December of each year.
2. An active file of available biologists which may be consulted at any time.
3. A Placement Office at the AIBS Conventions where an employer may interview candidates.

Subscription to AIBS Placement List: $1.00 per copy.

USES AND ADVANTAGES OF THE NSF NATIONAL REGISTER OF SCIENTIFIC AND TECHNICAL PERSONNEL

Since all information provided by the registrant is punched on IBM cards, statistical runs are easily made. Some of the uses of this information are:

Salary—the government rectifies inequities in salary between persons employed in industry and in government by using these figures as the basis for recommendations to Congress for salary raises;

To pinpoint deficiencies of trained personnel in certain disciplines;

As a base for selection of the best qualified candidate for:
Chairmanship of committees,
Receipt of travel grants to attend symposia, international congresses and other scientific meetings,
Consultancies.

The Register has been in operation since 1953. Of a possible 60,000 registrants in biology, only 30,000 have responded and only 20,000 have been eligible for inclusion in the Register. Needless to say, the greater the number of biologists registered, the greater will be the value of the Register to the individual biologist, the various participating societies and to the field of biology as a whole.

A new questionnaire has been compiled which corrects deficiencies discovered in the earlier form. ALL biologists, whether registered or not, are being sent a copy. PLEASE COMPLETE AND RETURN YOUR NEW QUESTIONNAIRE PROMPTLY!

(In writing to advertisers, please mention the journal—it helps.)

VOL. 32, NO. 2 June, 1957

THE QUARTERLY REVIEW of BIOLOGY

ONTOGENY OF PHYSIOLOGICAL REGULATIONS IN THE RAT

By E. F. ADOLPH

Department of Physiology, School of Medicine and Dentistry, the University of Rochester

INTRODUCTION

Physiological Regulations

AN INDIVIDUAL developing from egg to adult manifests its most obvious growth in size and shape. Behind the visible changes are many invisible ones, such as the acquisition of new chemical constituents, new capacities for sensation, and new ways of using energy. Least visible of all is the development of controls over one process after another, that is, the development of various means by which processes, instead of conflicting, fit into a pattern of continuous living. The aim of this investigation is to outline some of the ways in which such controls or regulations develop in an animal.

A living body maintains itself. When unable to do so, it no longer lives. Such is the general rule, as observers of unresting organisms see it. Recognizing this rule, biologists inherit the task of finding out the methods by which any kind of organism keeps going. Those methods are the foundation of its existence, an existence belonging to a man, or a bacterium, or a tree, or an insect. Existence is automatic with each of them. How they continue to live can be partly understood if we are willing to study the processes of movement and chemical transformation and excitation, and many another. Physiologists, observers of such processes in living beings, expect also to find that every process is under internal control. Muscles do not contract at random, but only when "told" to contract by means of a message through a nerve. A sweat or salivary gland does not secrete steadily but responds to particular nervous, chemical, or mechanical influences. The rule seems to be that all processes are dependent upon the state of the organism, that each process automatically fits its speed in some degree to whatever is happening in the body. That the process varies in relation to other events is the fact of its regulation. Though the pattern of regulation differs from one process to another and from one kind of being to another, adequate control is universal.

Some processes are characterized by steadiness in the midst of change. Their regulations are illustrated in the ceaseless adjustments whereby an animal breathes adequately even while it sleeps, or in the governed exchanges whereby an animal has the same composition year after year without retaining many of the same molecules in it. Other processes, equally regulated, are turned on and off in response to circumstances. Alimentary movements are largely absent until food arouses them; nerves carry no impulses until they are excited. Both kinds represent indispensable controls; kinds that we shall look for in the investigation here set forth.

Growth of Regulations

When I was studying the patterns of physiological regulations, beginning some twenty years ago, I wondered how a given pattern came into action. However satisfying it was to see the completed pattern in operation, the question kept recurring,

is it possible to find an uncompleted pattern in immature animals? Everyone knows that a newborn infant has deficient control over posture, movement, and body temperature. Eventually I looked for such incompleteness, choosing urine flow after water-loading as the phenomenon to be observed. I found a perfect illustration of a developing pattern, for newborn dog pups did not respond to water excess with a water diuresis, whereas after a few days of further development, they acquired such a response (Adolph, 1943). The water diuresis thus acquired could be regarded as a portion of the body's regulation of water excess. I had hoped then to extend the study to a number of regulated functions, but not until recent years have I been able to do so; here are results that describe in part how such controls develop.

In planning this investigation of emerging regulations, I found it expedient to pick one species (rat) on which most of the studies had been or would be performed. Within a species, a schedule or development of several regulations in relation to one another could be described. The advantages of concentrating upon one species will become apparent.

The present effort to understand the manner in which regulations or controls develop has an analogy. To understand a given machine one could walk along the assembly line and see the steps by which the parts of the machine are put together. By a similar method one may hope to understand physiological regulations. The parts in this case are not always visible structures, but they are elementary processes that, when combined in a particular way, do something which they did not do separately. We will watch a function as its elements become available for use in the living fetus or infant. We shall see that the function at successive stages can operate little or much. We shall recognize some of the contributions made to the whole function by individual processes acquired by it. Unable himself to be a creator, the scientist can watch creation going on. He will thus see the accretion of partial processes as they begin to participate.

The plan of watching regulations develop was used in the following example. The heart was removed from an animal such as an infant rat and laid in a dish. It continued to beat for many minutes. The frequency of its contraction was governed by several factors, one of which was temperature. Another heart, within the body of the infant rat, was found to beat at every temperature with the same frequency as the one isolated (Adolph, 1951). But in the adult rat, the intact heart beat faster at high temperatures, and slower at low temperatures, than its isolated counterpart. This fact was evidence that controls over beat-frequency were furnished by the adult body through mechanical, nervous, and chemical influences which were not present in early life. Of course, their development was traced in order to discover when they arrived, and to find whether they reached the adult pattern in one step or in several. In actual fact, the beatings of isolated hearts did not differ with age after birth; only when controls extrinsic to the heart were being exerted was there an influence of age.

It should be understood that in this work we are not drawing up an exhaustive account of the development of single physiological processes, such as heart-beats. We are selecting those few portions of the story of development that show most clearly those controls which appear at successive stages of physiological ontogeny. We are trying to describe or reconstruct the working organism from one aspect, namely, how its processes come to be regulated.

The ontogeny of physiological regulations can be studied now largely because specific patterns of regulation have been identified by previous researches upon adult animals. By following these patterns, we can search for their first appearance and their subsequent changes in immature organisms. I know of no other way in which the beginnings of particular regulations could be identified in the young. We trace backward with greater hope of recognizing a significant development than if we trace forward with no foreknowledge of the adult state.

Types of Regulatory Relations

Since we come to the study of regulatory arrangements in infant animals from the investigation of the patterns of regulation that prevail in adults, we do well first to look for comparable patterns in infants; the kinds of information that were then useful may be the very kinds we now need. Actually, five types of relations were found to describe regulatory activities (Adolph, 1943); an example of each may be mentioned. (P) Exchanges of some component varied with excesses or deficits of it. Thus, water was excreted faster when it was present in excess. This familiar observation furnished an important part of a pattern characteris-

tic of many kinds of animals. (Q) Concentrations of a substance in the body varied with concentrations of the same substance outside it. In this fashion, more oxygen in the surrounding air tended to increase the pressure and concentration of oxygen in the body. But the two increases were not equal, for certain controls—such as breathing—modified their relation. (R) Variabilities of the amounts or intensities of a particular substance or property showed what departures from constancy were allowed by the pertinent controls. Thus, a great variation of glucose concentration in plasma indicated less precise controls than did a small variation. (S) Forms of behavior that were aroused by excesses or deficits of a given component were obviously parts of the compensation for excesses or deficits. For instance, locomotion toward a source of heat was a part of the regulation of body-heat content in cold surroundings. Finally, (T) individual processes and structures were utilized in the animal's responses to deviations in bodily properties. Effectors, transmitters, and sensory devices were the elements from which these responses materialized. In this way, temperature sensations and endocrine secretions represent processes or means by which constituent parts of regulatory patterns are executed.

Each of the five types of relations corresponds to a concept of what regulations are and how they may be described. We thus have considerable guidance as to what varieties of relationships to look for in developing animals. Conversely, the study of regulations in developmental stages now reveals patterns of self-regulation in various stages of complexity. Some regulations, such as certain portions of those governing energy transformations, never cease from germ cells to adults. Others, such as those controlling the circulation of the blood, are absent for a period while the embryo develops, but particular constituent processes appear at definite periods thereafter.

Background

As we survey the general field of physiological ontogeny, we recognize that only by means of diverse observations upon development have the broad facts of orderly change been established. We find ourselves relying upon the pioneer researches of many diligent students, especially those who dealt with mammals, of whom we can name: Preyer (1885), who watched the beginnings of activities in parallel organ systems; Cohnstein and Zuntz (1884), who measured the oxygen that the fetus respires; Donaldson (1924), who envisaged growth as a multiple process; Barcroft (1947), who opened men's eyes to processes of prenatal life; and many another pioneer such as Flexner (1941), Needham (1942), Nicholas (1947), Clement Smith (1953), and Windle (1940), some of whom have formulated their concepts in monographs; and others who have participated in recent symposia such as the one at Cold Spring Harbor (1954) and at the Czechoslovak Academy of Sciences (1956). Since we are here describing not the development of processes, but the development of regulations, we will limit our study to some of those processes and relationships known to take part in a regulatory operation.

Further, we are not now examining that control of development itself whereby each individual traces a course like its siblings. That is the kind of regulation ordinarily meant by embryologists who study the genes and organizers that steer development. Instead we wish to trace the stages by which are achieved those physiological regulations which result in steady or unsteady states of the individual. Some of the above investigators incidentally mentioned regulatory activities in the sense of the term used by Bernard (1878), namely, "arrangements of the organism such that external variations are compensated and equilibrated." Thus, Preyer (1885) supposed that "no embryo possesses a heat-regulating mechanism," although he and predecessors had noted the guinea pig's capacity for self-maintenance of body heat immediately after birth. Barcroft (1947) observed many regulatory responses in prenatal circulatory and respiratory functions without explicitly emphasizing their contributions to maturing maintenance. Cannon (1932, p. 284) recognized that "homeostasis" of heat and of glucose develops gradually even after birth, but he did not measure the degrees of their control at various ages. My study of maturation of water diuresis in infant dogs (Adolph 1943, p. 269) demonstrated that even after birth, regulations are not "fixed properties of unchanging organisms." Clearly the task remains of surveying systematically the development of bodily maintenance.

Plan of the Investigation

When we recount a few portions of development that contribute to the regulations characteristic of adults, these portions cannot ultimately be considered apart from other portions; but we have to

limit our study somehow. No doubt the animal is a going concern at all stages of growth; all stages have (more often than not) a sufficient complement of regulatory activities by which to operate. We may hope that the regulations of immature stages can be understood as thoroughly as those of the mature one.

By limiting most of the studies pursued here to a single species, we can deal with quantitative data, all of which will be interrelated when we place them upon one age scale. The laboratory rat has already been used as much as any other one species for the study of developmental phenomena; for data we can therefore rely partly upon forerunners. Whenever additional species are mentioned, we must bear in mind that they have other rates of development, other body parameters, and other correlatives. We then temporarily lose the quantitative setting.

As we study the development of physiological regulations in the growing individual, shall we find that regulations start from nothing? Can we see their origins? It turns out that both (a) beginnings of a novelty, and (b) modifications of a continuity are to be found. We can see regulations operating in various stages of incompletion, much as we can test the performance of an engine before installation of all of its parts.

We shall realize that a huge portion of physiological ontogeny is postnatal. Though regulatory activities are instituted at all stages of development, some of them can be demonstrated only so late in life as the young animal that has come free from its mother.

Heat, oxygen, and water are the components of rats for which regulations will be described. They are selected chiefly because solid data and relations are available about them in adults, and because adequate methods of study can be applied. In their description we shall be concerned with many structures and many chemical reactions. The brain, the blood, the kidneys, the placenta, enzymes, metabolites, and translocations will all share our attention. Certain interrelations among components and processes are the patterns we seek. In the end we shall also be able to find general patterns and general characteristics among the regulations of the several components.

If a fetus or an infant were suddenly endowed with awareness, it might forebode its future and ask: How shall I know when to heat up my body? What will tell me when to breathe faster? What shall I do if I get short of oxygen? When will my kidneys need to excrete salt faster? Will I know whether my extracellular fluid needs replenishment? Physiologists believe that the fetus does not worry; we also believe that management of its functions is vested in controls that do all those adjustments without knowing how. It is we, not the rats, who want to know what is done to manage those functions, and how.

An Age Scale

Our specific task is to reconstruct what is known about certain constellations of physiological properties as they progress with age. In order to interrelate them we shall be compelled to oversimplify and to schematize the events. In order to relate diverse changes in the constellations, we place many measured activities upon a common scale of time. But rat age as ordinarily reckoned from birth serves less well than as reckoned from conception or fertilization, for part of the progress is prenatal, part is postnatal, and no interruption is visible at birth. We will consider fertilization as zero age. By using conceptual age, we will deal with only one scale of ages, and this will emphasize the continuity of development even though we may minimize the important transitions from prenatal to postnatal life. Whenever we compare dated events in more than one species, we have no commensurate age scales; the variable event of birth itself (as in comparing opossum and chinchilla) would be one of the many incongruities.

While fertilization marks a time to which all developments may conveniently be referred, it is not directly observed. Coitus of parents and birth of young are commonly the actual recorded data. Careful study has revealed that rats enter estrus and begin to mate 7 to 11 hours before ovulation is due (Blandau and Soderwall, 1941). Fertilization occurs within the period 2 to 5 hours after ovulation (Braden and Austin, 1954; Austin and Braden, 1954). Altogether 12 hours elapse on the average between coitus and fertilization. Actual gestation lasts a mean of 21.3 days from fertilization, with a recognized variability. For present purposes, these times are accurate enough, except when gestation is shortened or lengthened by lactation or other controlled circumstances (Nicholas, 1949). In the end we should see a time-table of coordinated development, a development that provides the growing individual with controls which operate throughout the life span.

HEAT REGULATION

Gradual Development

A newborn rat is often said to be without control of its own body-heat content or temperature. Roughly this is so, and therefore we can observe the development of this regulation postnatally. Later we will project certain concepts backward into the stages before birth, and will realize that the beginnings of control were already there.

Regulation of the body's heat content is acquired gradually. This fact is readily evident from a simple comparison of body temperatures with air temperatures after exposure (Fig. 1). Body temperatures of infant rats are measured by inserting fine thermocouple wires either into the colon or the peritoneal cavity. A junction between wires of two different metals thus resides deep in the body, and the electrical potential produced there is compared galvanometrically with that produced at a symmetrical junction kept in melting ice.

In newborn rats the temperatures of body and of air are nearly identical after an hour of exposure; at later ages the difference of temperatures becomes greater, and at 73 days of age the colonic temperature is, within wide limits, independent of the surroundings. The temperature diagram, belonging to regulatory relations of type Q, represents the overall result of distinguishable factors. Our task is to present a scheme that will identify and gather together the various physiological activities that participate in the regulation, and to describe some of these participating processes and factors so far as we think we recognize them. Like the accountant, we can have separate pages for gains and for losses of heat.

Heat Production

Oxygen Consumption

Every organism produces heat; and regulation of body heat, which usually maintains an internal temperature considerably above the temperature of the surroundings, consists in the conservation or retention of some of that heat in the body. Ordinarily an infant lives aerobically, so that, as for adults, oxygen consumption may be taken as the full measure of heat production.

For the rat, oxygen consumptions have been measured at several prenatal stages. Consumption by blastocyst embryos is measured by means of a sensitive Cartesian diver (Boell and Nicholas, 1948); the technique for its use will not further be indicated here. Oxygen consumption in later ages is usually measured by enclosing an infant rat in a flask through which air is circulated (Antoschkina, 1939). As oxygen is removed by the rat, and carbon dioxide is removed by a chemical absorber, measured oxygen is added to replace it. Another method is to place the animal in a closed respirometer chamber of which the volume decrease is measured —the very method that serves routinely for tissue slices (Kleiber et al., 1943; Fairfield, 1948).

The data obtained (Fig. 2) suggest that the oxygen consumption per unit of tissue weight or of body weight is smallest some days after embryonic cleavage has begun, and possibly after implantation of the embryo in the uterus. The embryos had to be isolated before their metabolisms could be measured, and the disturbances so imposed may or may not have made the results unreliable. In any case, minimal oxygen metabolism proceeds uninterrupted, yet at changing rates, from dormant ovogonium to thriving fetus. Even for the minimal or resting state the self-contained controls that determine the steady rate of oxidation are largely unknown.

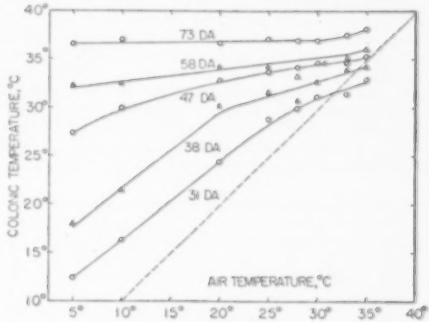

FIG. 1. COLONIC TEMPERATURE IN RELATION TO AIR TEMPERATURE AT END OF 1 HOUR OF EXPOSURE OF RATS OF VARIOUS CONCEPTUAL AGES (Data of Antoschkina, 1939.) This diagram illustrates regulatory relations of type Q.

Immediately after birth the oxygen consumption is probably higher than in the fetus. For purposes of securing these data on oxygen consumption, the temperature of the infant is controlled by external warming in order to have the tissue temperature uniform at all ages. When this is done, a second decrease appears about ten days after birth, followed by a temporary rise at one month (An-

toschkina, 1939; Kibler and Brody, 1942). After three months, the resting metabolic rate decreases and subsequently declines gradually into old age (Davis, 1937).

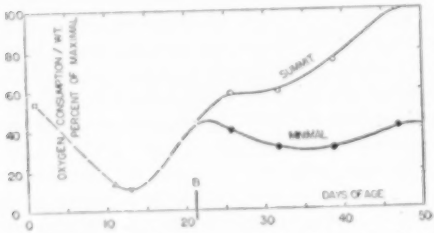

FIG. 2. OXYGEN CONSUMPTION PER UNIT OF BODY WEIGHT AT VARIOUS AGES

Minimal = at rest; Summit = cold-exposed. Maximal consumption in shivering (at 47 days) was 11.0 ml. oxygen per kg. min., here designated as 100%. Sources: 1-day, Boell and Nicholas (1948); 11-day, Negelein (1925); 13-day, Kleiber et al. (1943); postnatal, Antoschkina (1939). Portions of the postnatal measurements were closely confirmed by Gelineo (1934), Gulick (1937), Davis (1937), Kibler and Brody (1942), Fairfield (1948), McCashland (1951), and Grad (1953).

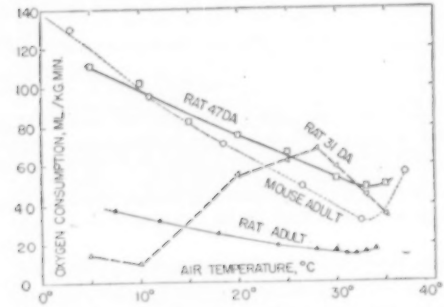

FIG. 3. HEAT PRODUCTION IN RELATION TO AIR TEMPERATURE AT END OF 1 HOUR'S EXPOSURE IN RATS OF THREE AGES (data of Antoschkina, 1939), AND IN ADULT MICE OF THE SAME BODY WEIGHT AS THE 47-DAY RATS (data of Hart, 1950)

Extra Metabolism in Cold

From birth onward we may compare with the resting metabolic rate the faster rates that may be aroused when we place rats in diverse air temperatures, measuring their oxygen consumptions in each (Fig. 3). In the adult, much more heat is produced in cool surroundings; the ratio between the maximal ("summit") heat production in response to any cold surroundings and the minimal or resting heat production in warm surroundings ("neutrality air temperature") is the "metabolic quotient" of Giaja (1925).

At ages up to 24 days, no stimulation of excess heat production by the presence of cold air can be found (Fairfield, 1948), but soon thereafter (Fig. 2) a slight increase is registered. Between 26 and 38 days, however, a steady state of heat exchange rarely prevails in cool surroundings, and the net oxygen consumption is a resultant of (a) cold stimulation whereby more heat production is aroused, and (b) tissue cooling whereby the capacity to produce heat is reduced. Subsequently, the response to cold environment is enhanced, and at 47 days is maximal. At this age, the metabolic quotient (ratio of maximal to resting) of 2.5 is as high as in the adult; thereafter both the maximal and the minimal heat productions decline in intensity with age.

Oxygen consumptions during cooling may be related with body temperatures that prevail (Fig. 4). Such correlation shows that heat production is stimulated to greater intensities until the body temperature has fallen below 30 or 27 C. Use of these data to represent body temperature is slightly inaccurate because colonic temperatures alone are known, and they only at the end of the period of cooling and of measured heat production. Further, the rats in this series older than 47 days were probably not exposed to surroundings cold enough to elicit their maximal productions of heat; in this respect our information is incomplete.

The extra heat production that is aroused by cold air probably arises in muscles at all ages. This shivering is evidently absent at birth; one might even suppose it would be futile, wasteful, and dangerous if infants' stores of energy were depleted in that way. The effector muscles are present at birth; they have contracted and are capable of activation by their motor nerves. Their failure to respond to cooling depends upon some sensory or central factor which develops after 25 days, and visibly after 30 days (Gulick, 1937). Where and what that factor or factors might be requires investigation.

Heat Loss

Insulation

We next inquire, what goes into thermal independence, beside the production of extra heat upon demand, which we just examined? Or, in terms of Figure 5, what changes allow the colonic temperature to stay progressively higher (in C),

what changes assure summit metabolism at progressively lower air temperatures (in D), and how does the neutrality temperature progressively decrease (in E)?

Heat loss depends upon at least two recognized factors: the presence of external insulation (skin and hair) and the geometrical proportions of the body.

Skin and hair begin to grow considerably before birth, the first hairs appearing on the surface of the skin after birth. At 16 days of conceptual age, the epidermis thickens from a single cell layer by multiplication of cells (Fraser, 1928). With great speed the thickness increases about 20-fold by the time of birth, and thickening continues unabated for several days thereafter. The epidermis develops in several cycles of 35 days each, with thinning of the skin during half of each cycle (Butcher, 1934). Per unit of dry weight, the skin consumes oxygen fastest during the thin phase (Butcher, 1943). In the same phase, the water content of the skin is greatest (Butcher and Grokoest, 1941). Per unit of wet weight, the histamine concentration of the skin also is temporarily elevated as compared with the moderate steady concentration which was suddenly attained in the three days before birth (Hardwick, 1954). Evaporative loss of water from the surface of isolated skin keeps in phase with the high water content and the high oxygen consumption (Butcher, 1954).

Hair undergoes a development paced by the skin. Hair germs appear as soon as the epidermis thickens from a one-cell layer (Fraser, 1928). Hair pegs and hair bulbs appear by the time of birth. The first hairs erupt from the skin surface in the second day after birth. Dorsal hairs erupt a few days before ventral ones (Fig. 6). They grow in length during 18 to 20 days and then cease to elongate (Butcher, 1934). This is the postnatal period during which insulation accumulates to the point where a balance of heat exchanges can be achieved without the aid of a nest or a mother. The subsequent history of hair development is that the hair follicles rest from the 40th to the 56th days. Then the second cycle of growth develops adult pelage alongside of the infant hair coat. Subsequent cycles add longer hairs to those already present. Thus the total external insulation comes into existence on a skin 200 times as thick as the early fetal epidermis.

Genetically hairless rats acquire in infancy a normal first coat of hair, which however is lost at weaning time; partial hair regeneration takes place, and some hair follicles form cysts which thicken the skin (Thigpen, 1940). In hairless rats and other hairless mammals and featherless birds subjected to

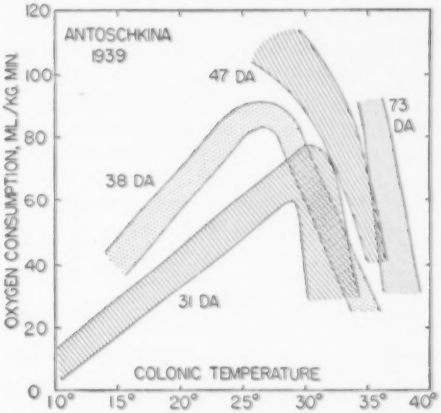

FIG. 4. OXYGEN CONSUMPTION IN RELATION TO FINAL COLONIC TEMPERATURE IN INFANT RATS OF FOUR AGES

Conceptual ages are indicated in days. Each band includes the means of 21 groups (of about 5 individuals each) separately exposed to air of controlled temperature. The younger rats cooled more than the older ones, as Fig. 5 also shows. (Data of Antoschkina, 1939.) This diagram represents a small portion of a regulatory relation of type P.

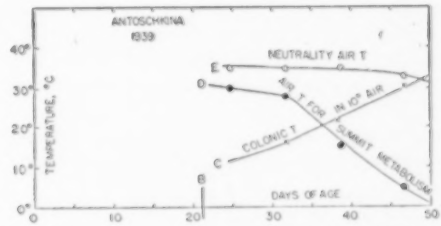

FIG. 5. AIR TEMPERATURE OF NEUTRALITY (MINIMAL OXYGEN CONSUMPTION), AIR TEMPERATURE OF SUMMIT METABOLISM (HIGHEST OXYGEN CONSUMPTION ELICITED BY AIR OF ANY TEMPERATURE), AND COLONIC TEMPERATURE OF RAT AFTER SOJOURN OF 1 HOUR IN AIR OF 10° C

(Data of Antoschkina, 1939.)

excessive cooling, the whole heat production system is continually stimulated as a sort of compensation. This includes hyperfunction of the thyroid and adrenal glands, increased food consumption, and increased blood circulation (Landauer, 1932).

A balance of body heat at a temperature considerably above the environmental one does not

exist in any small animal without external insulation. Hair, for an infant rat, is a number-one prerequisite for easy self-maintenance of body heat. Hence its history is part of the story of heat regulation. Heat regulation can be better understood if we relate the development of hair structure to the timing of events in the skin and to all other elements of thermal exchange. The total hair weight

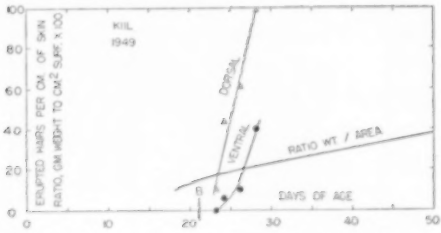

FIG. 6. HAIR COUNTS AND RATIOS OF BODY WEIGHT TO BODY SURFACE IN RATS OF EARLY AGES

Hair counts were made in skin sections by Kiil (1949) in two dorsal and two ventral areas. Ratios were estimated from data of Donaldson (1924), and Lee (1929).

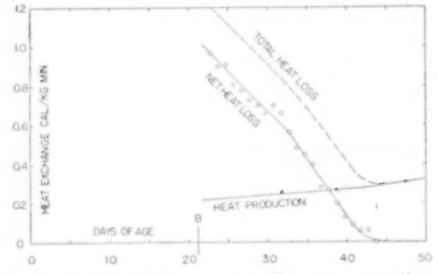

FIG. 7. HEAT EXCHANGES IN RELATION TO AGE, DURING INITIAL 15-MINUTE EXPOSURES TO AIR OF 15° C

Heat production or total heat gain from data of Antoschkina (1939) in our Fig. 4. Net heat loss estimated from data of Brody (1943). Total heat loss = heat production + net heat loss.

would be a useful index of the insulation value, which needs to be measured directly.

Surfaces

The ratio of body weight to a body surface area may serve as a rough guide to other factors in the conservation of body heat (Fig. 6). The familiar estimates of surface area assume that the shape and proportions of the body do not change—which is only approximately true—and that posture is uniform through life. The estimates serve to show that proportions change too slowly to account for the gain of heat control at 47 days, but that hair growth dominates heat conservation by that age.

Cooling Rates

Another contribution to the understanding of heat loss comes from the direct measurement of cooling rates, as in Figure 7. Within periods of ¼ to ½ hour of exposure, drop of body temperature tends to be linear with time, and proportional to the difference in temperature between colon and air (Fig. 1). The latter relation corresponds to Newton's "law of cooling." The results show that the rate of cooling decreases linearly as age increases up to about 40 days of age. Linearity may be fortuitous, however. For infant rats in nests made by their mothers, linearity is not the rule. The importance of nests as protection against cooling in the absence of an adult rat is emphatic, for in 15° air (Gelineo and Gelineo, 1952) the rates of cooling of newborn rats when in nests were at most one-third as great as when the infants were not in nests, and by 37 days of age, cooling in nests was nil.

The actual heat lost from an infant rat would be difficult to collect in a calorimeter. Estimates of heat loss can be obtained by another method. Under conditions where no change of body temperatures occurs, we can state that Heat loss = Heat gain, and the gain is ordinarily the equivalent of oxygen consumption. When body temperature is changing, we rely upon an equation of balance, such that Heat loss = Heat gain + Heat unstored. Heat gain is all derived from oxygen consumption; heat unstored is the drop of body temperature times the heat capacity of the animal. Specific heat capacities are similar in most tissues; they have been measured for whole adult mice (Hart, 1951), and rats (Jacobson, 1954), and we may use the factor 0.83 cal./gm. deg_e in estimating the change of heat content of the rat. By use of the equation, we may relate heat loss to every one of the factors with which heat production was related above.

In computing cooling rates (Fig. 7) we use the first part of cold exposure, i.e., the first 15 minutes. But oxygen consumptions were measured only after 30 minutes of exposure (Fig. 4). We can however integrate the heat productions at each temperature while the body is cooling linearly; by this procedure the heat productions of Figure 7 are obtained. It turns out that heat loss per unit of body weight is actually greater at birth (22 days)

than at any subsequent age. Only after age 42 days does the young rat manage to have a heat loss in cold air which can be equalled by its heat production.

Two further points may be mentioned as important aspects of the infant's regulation against low body temperatures. The first is that the infant tends to move toward the mother and to maintain contact with her. This behavior (a regulatory relation of type S) is such as to minimize heat loss from the infant. It is just as successful in avoiding lowering of heat content of the body as in any behavior on the part of the mother (such as providing nest or seizing young). It could be supposed that infant rats are attracted to the mother by stimuli other than warmth; if so, the result is still a contribution to heat regulation. Probably behaviors of mother and infant reciprocate and mutually reinforce each other. Experiments are needed to ascertain whether heat alone will (a) cue to orient and move the young toward its source, or (b) make the infant content to stay in warm surroundings once it chances to contact the warmth.

The second point is that regulation may be measured by the variability of body temperatures (regulatory relation of type R). Everyone knows that the infant rat has smaller and slower variations as it progresses from birth to weaning. A collection of randomly-ascertained colonic temperatures would illustrate the diminishing variability as the rat matures. For, the narrower the variations, the more operative are the processes that prevent departures from the preordained and guarded mean.

When heat gain and heat loss are considered together, there seems to be no way of deciding whether the heat production ordinarily paces the heat loss, or the reverse, or neither. Early development of the rat fixes the basal rate of heat production; later, the facultative heat, including that of shivering, is added to it; and still later, the rate of heat loss diminishes to a value that can undercut it. From then onward, management seems to consist in juggling the two rates from a common operating control.

Almost nothing is known about the development of regulations that operate in *high* environmental temperatures. Adult rats have but small protection against overheating (Adolph, 1947) although evaporative loss augments 4-fold over the usual (Black and Swift, 1943). This loss is primarily through panting, which is slight indeed compared with that of adult carnivores. Other responses to warmth, such as sprawling posture, also develop at some age after birth.

Heat Contents

The rate of heat production is quantitatively related with the heat content of the rat. For, if we recognize that the body temperature (Fig. 4) is proportional to body-heat content, we conclude that at each age the heat production increases when the heat content begins to fall. That relation clearly represents a regulatory control over heat exchanges. It constitutes part of an "equilibration diagram," which portrays regulatory relations of type P. It tells us that higher heat content will be recovered whenever the total heat loss becomes less than the measured heat production characteristic of each body temperature. Eventually we should hope to complete a heat-equilibration diagram for each age of the rat.

Comparison of heat losses and heat productions in diverse body or environmental temperatures shows to what extent heat balance or body-temperature maintenance can be achieved. Acquirement of complete heat regulation may be viewed as consisting of two separable factors; the development of capacities for attaining heat productions as great as heat losses, and the development of responsivities whereby the capacities are utilized. Whenever heat production (Fig. 3) actually equals heat loss, body temperature is maintained. Most of the obvious change with postnatal age is in the capacity for decreasing heat loss. Less obvious is the change of responsivities, and these will next be explored.

Devices in Regulation

Nervous Factors

Studies of heat regulation in adult rats tell us what kinds of regulators to look for in infant rats. Specifically we may seek some that become operative before 70 days of age. We here concentrate our search on the nervous system and the endocrine system.

The brain attains most of its growth relative to the whole body before birth (Fig. 8). Postnatally (35 to 40 days of age) there is a sudden increase in vascularity (Fig. 9) and a great deposition of myelin (Fig. 10), the latter being measured specifically in the hypothalamus where nervous connections subserving heat regulation, among others, are

known to exist. At the same time, the composition of the whole brain is changing rapidly, accumulating compounds such as phosphocreatine (Fig. 11) that were absent at earlier ages. This fact suggests

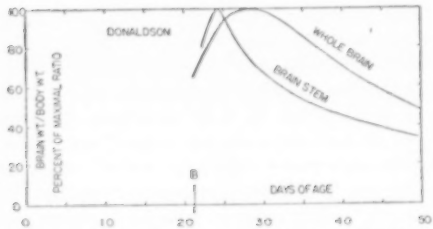

FIG. 8. BULK OF BRAIN AND OF BRAIN STEM RELATIVE TO BODY BULK AT VARIOUS AGES IN RAT
The maximal ratios occur at 28 and 24 days of age. (Data of Donaldson, 1924.)

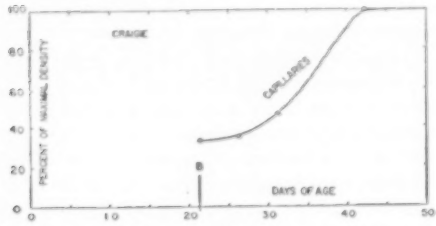

FIG. 9. NUMBERS OF CAPILLARIES PER UNIT OF VOLUME OF BRAIN STEM GRAY MATTER
(Data of Craigie, 1924.)

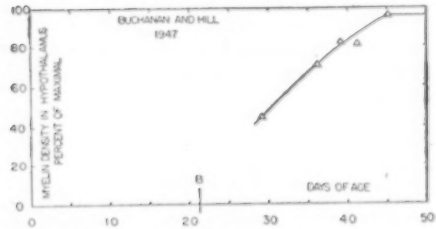

FIG. 10. DENSITY OF MYELIN IN HYPOTHALAMUS IN RELATION TO AGE
Two litters of rats were used, one individual being killed for microscopic preparation at each point. (Data of Buchanan and Hill, 1947.)

that there is activation of enzymes that were not evident before, and actually a great variety of enzymes have been identified, all increasing with age in abundance and concentration. Possibly the ones that increase most suddenly, such as those concerned in phosphorolysis, are most likely to be concerned in functional developments of the sort discussed above. However, the changes of composition have been studied in the brain as a whole, or in the cerebral hemispheres; whereas we should like to draw our correlations with highly local and specific changes in a small region of brain stem or of the hypothalamus in which few biochemical and no physiological events have been identified. The many correlations that might be drawn between heat regulation and the data of Figure 11 would be uncontrolledly speculative at present.

Adrenal Activities

The adrenal glands may contribute to heat regulation both through the cortex and through the

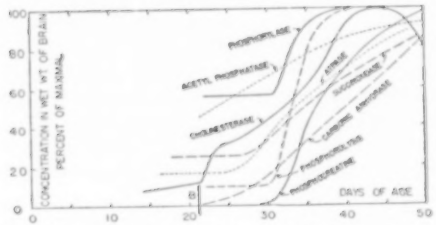

FIG. 11. DEVELOPMENT OF SOME ENZYMIC ACTIVITIES AND PRODUCTS OF BRAIN AS MEASURED IN MINCE FROM WHOLE RATS OF DIVERSE AGES
All per unit weight. Phosphorylase and Phosphorolysis (Shapiro and Wertheimer, 1943). Succinic dehydrogenase and Adenosinetriphosphatase or ATPase (Potter, Schneider and Liebl, 1945), Cholinesterase (Metzler and Humm, 1951), Carbonic anhydrase (Ashby and Schuster, 1950), Acetyl phosphatase (Ashby, Garzoli and Schuster, 1952), Phosphocreatine (Mandel and Bieth, 1951).

medulla. The adrenals can be completely destroyed by cautery at 17 days of fetal age without diminishing body growth (Tobin, 1939). When one adrenal is destroyed, the other hypertrophies. Total destruction leads to hypertrophy of parathyroids and greater activity of pituitary, thyroid, and thymus. The adrenals as a whole are relatively largest at 28 days of conceptual age (Donaldson, 1924); most of their tissue is cortex (J. C. Donaldson, 1919). But at birth the medulla occupies a larger proportion than at any later age. The content of catechol hormones is increasing throughout infancy; if the catechol is considered to be segregated in the medulla, the concentration there before birth is only one-sixth of that in the adult rat, increasing linearly during the first two postnatal weeks (Hökfelt, 1951). Of the catechols, none is epinephrine at 17 days, but by the time of birth half is epinephrine, and the fraction represented by it continues

to increase. The remainder is largely nor-epinephrine which becomes relatively less abundant.

Adrenal cortex may mediate some of the rat's responses to cold air. Secretion of its hormones occurs by 20 days of conceptual age (Josimovich et al., 1954). At four days after birth, and possibly before birth, the adrenal glands become enlarged (Moon, 1940) and partially depleted of ascorbic acid (Jailer, 1950) when stimulated by injection adrenocortico-tropic hormone ACTH, but not by cold exposure nor by injection of epinephrine (Fig. 12). A few days later, depletion occurs in response to epinephrine but still not to cold air. At 35 days, partial depletion also follows cold exposure. Further, it may be inferred, as for the adult rat (Long, 1947), that cold exposure leads to epinephrine liberation from the adrenal medulla, and epinephrine in turn induces liberation of ACTH from the pituitary gland in amounts that influence the manufacture and secretion of a hormone whose formation involves ascorbic acid. The presence of ACTH can be demonstrated in the pituitary even at 26 days of conceptual age (Rinfret and Hane 1955). The experiment of Figure 12 shows that the adrenal cortex is ready to secrete hormone at the first stage, the anterior pituitary is ready to put out ACTH in response to epinephrine at the second stage, and the adrenal medulla is ready to part with epinephrine in response to cold exposure at the third stage.

At the same time that the adrenal medulla is refractory to stimulation by cold exposure, the end effect of cortical hormone is still missing (Holtkamp et al., 1949; Irwin et al., 1950). Adrenalectomized infant rats cool much more rapidly than intact ones, even as do adults. Administration of adrenal extracts do not slow the cooling until the 37th day of age, the very age at which the adrenal cortex itself decreases its ascorbate content in response to cold exposure. It may be inferred that the prevention of cooling, perhaps by increase of heat production as well as by reduction of heat loss, becomes tuned to the cortical hormone at the same age that the adrenal cortex agrees to furnish hormone when specifically stimulated.

Altogether, we analyze heat-regulatory activities (relations of type T) by observing the constellations of properties and capacities for response, as they are added to, day by day, during growth. No sudden spring to action occurs anywhere. But the over-all effect builds to a maximal regulation that is maintained for life.

The tolerance to low body temperature dies away during a postnatal period of three weeks, the very period during which heat loss is diminishing (Fig. 7). As far as we know, high tolerance and complete control of body-heat content do not coexist. Could it be that close management of heat exchanges is gained at the expense of tolerance? In what sort of system might the two regulations conflict? Whether change in tolerance itself determines, or is linked to, the change in latitude of heat loss and heat production might be ascertained whenever a method is found of hastening or retarding change.

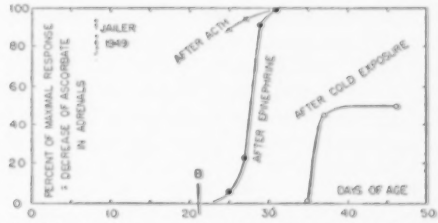

FIG. 12. RESPONSES OF ADRENAL GLANDS TO THREE STIMULI GIVEN TO INFANT RATS

Responses were all measured as decreases of ascorbic acid content relative to unexposed control individuals of the same age. Maximal response was a decrease of 38 percent. (Data of Jailer, 1950.)

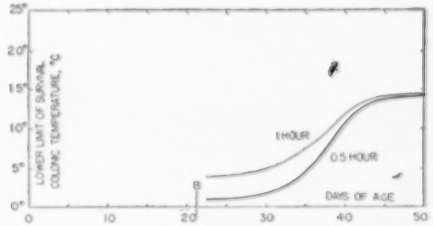

FIG. 13. LOWER LIMITS OF COLONIC TEMPERATURE THAT ALLOW SURVIVAL OF INFANT RATS EXPOSED TO IT IN AIR FOR ½ OR 1 HOUR

(Data of Adolph, 1948.) Survival was judged by spontaneous recovery of breathing when artificially rewarmed.

Lethal Body Temperatures

Tolerance to Cold

The infant rat survives body temperatures down to 1°C. (Fig. 13), while the adult rat under most circumstances is killed at about 15°C. Many processes (heart-beats, breathing, nerve conduction) become modified with age, all losing their

abilities to operate below 10° to 15°. All the modifications are gradual, and it could be that all are governed by a single, limiting influence.

Recovery of infants when rewarmed from such a low body temperature depends in part upon the availability of oxygen during the hypothermic period. But temperature has a limiting effect of its own, for survival is shorter as the temperature falls below 10°, whereas oxygen itself is used less rapidly at 1° than at 10°.

Consideration of the partial processes concerned

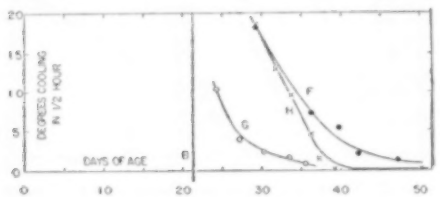

FIG. 14. RATES OF INITIAL COOLING OF INFANT RATS OF DIVERSE AGES WHEN PLACED IN AIR OF THE TEMPERATURES AND OTHER CONDITIONS INDICATED
Sources of data: Buchanan and Hill, 1947 (F), Gelineo and Gelineo, 1952 (G), Holtkamp et al., 1949 (H). Similar data have also been furnished by Antoschkina (1939) and Brody (1943).

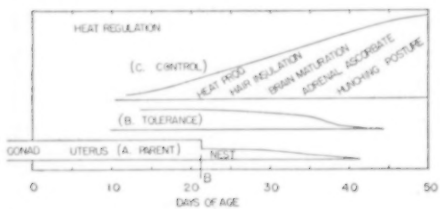

FIG. 15. DIAGRAM SUGGESTING THE ROLE OF THREE TYPES OF HEAT REGULATION AND SOME OF THEIR SUBDIVISIONS, FROM BEFORE CONCEPTION TO 50 DAYS AFTER IT IN THE RAT

in heat regulation conjures before us the analogy of an incompletely-installed air conditioner. The newborn rat evidently has its power plant in place. It may lack sensory devices or connecting mediators that will activate the equipment when stimulated. We need merely note that operation of the apparatus is almost worthless before all its parts are functioning. Yet the parts fit an effective working system when they finally mature.

Succession of Controls

A developmental succession can be discerned. The change of lethal limit of temperture with the age of the rat leads us to distinguish three sorts of control or regulation over the survival of infant rats in relation to body heat. Regulation A is the maternal control by the mother's body temperature before birth, and by the mother's body and behavior in the nest after birth (Fig. 14). Regulation B is the constitutional tolerance to low tissue temperatures at birth and during three weeks thereafter. Regulation C is the sum total of the controls acquired by the postnatal rat. The course of each regulation is paced by a common time-clock which presumably starts to tick at fertilization (Fig. 15). At a given age the three may overlap.

At the stages of postnatal life in which heat regulation C is incomplete, the rat survives severe cooling (regulation B). In this way its tolerance to low temperatures of environment is great throughout life; in step with the progressive rise of its lethal temperature from 0° to 15°C. is the decrease of its likelihood of ever becoming that cool. One kind of regulation (C) has supplanted another (B). As yet there is no evidence that acquirement of regulation C is dependent upon loss of regulation B.

Heat regulation C is a luxury for an animal kept in an incubator, but is probably not optional in the lives of most mammals and birds. In all, some form of maternal protection constitutes regulation A, and operates along with B until regulation C has become available.

Ultimately we need to delve much farther in order to understand the development of heat regulations. We should inquire what kind of timing devices control the orderly sequence with which the constituent regulations become available, as well as the various tissue activities that make up each of them, such as shivering, temperature sensations, hypothalamic transmission, and hormone sensitivities. Some sort of pacemaker seems to furnish cues that synchronize a great variety of events.

Effects of Body Temperatures

On Pulse Rate

Not only do several factors and circumstances determine what the body temperature shall be, but also the body temperature influences reciprocally what many of the properties of the body shall be. The influences vary with the age of the individual. The most striking effect of low body temperature is the lethargy that prevails; body movements are slow, reflexes are suppressed, and narcosis supervenes. Quantitative data are availa-

ble at several ages and various low temperatures for heart-beat frequencies, breath frequencies, oxygen consumptions, and endurances of anoxia.

Heart-beat frequencies in rats of 37° body temperature increase during fetal life from the first heart-beats at 9½ days of age until birth (Fig. 16). After birth the resting frequency falls significantly, then it further increases up to 500 beats per minute. In adults the frequency is about the same as in newborns. In newborn infants, the frequency diminishes almost linearly with body temperature, persisting even at 5°. At 30 to 40 days of conceptual age, the frequencies are greater at all temperatures above 15°, and still decrease linearly with temperature (Adolph, 1951). But in the adults two differences are observed. The rate characteristic of the euthermic rat (37°) increases when the body first cools. Nevertheless, with further cooling the frequency decreases linearly with temperature. The limit is now reached at 12°, the heart stopping reversibly until the rat is artificially rewarmed from that temperature. Evidently the circulation of blood is variously affected by temperature at each age, yet it is regulated in such a manner that the circulation remains adequate for bodily maintenance within the wide ranges of temperature that are here mentioned.

On Breathing

Breath frequencies of newborn rats diminish with temperature (Adolph, 1951). At 30 to 40 days of age the relation has changed, for no diminution of frequency occurs at temperatures down to 27°. At these ages breathing continues down to 10°, while in the adult it ceases at 15°. Thus the effects of all temperatures upon the frequency of breathing shift with age. It may be mentioned that the ability to breathe has been suspected of limiting the ability of adult animals to survive hypothermia without assistance. If breathing limits survival in adults, it does not in infants, since it can cease and then spontaneously resume at rewarming. Much is yet to be learned about the nervous factors in performance of breathing at extreme temperatures, a performance that greatly differs in infants and in adults.

On Oxygen Consumption

Oxygen consumptions have been measured at various body temperatures both in infant rats and in adults (Antoschkina, 1939; Fairfield, 1948). Up to 24 days of age the consumption diminishes as the temperature falls. At later ages the consumption first increases with moderate cooling and then is progressively paralysed by further cooling (Fig. 4). This particular increase with falling temperature is considered a major part of the arrangements by which body heat is regulated. However, no sharp line can be drawn between participating arrangements and non-participating ones; for instance, pulse frequency and breath frequency are tied to oxygen delivery in such a way that all work successfully in a specified range at each temperature. For this reason it may be supposed that all or many of the "effects of temperature" are part of the regulatory picture that we are studying.

Survival of individuals without oxygen depends upon age (see Fig. 18, below), at all temperatures, as judged by the ability to breathe spontaneously

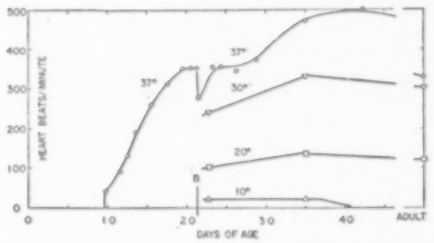

FIG. 16. FREQUENCY OF HEART-BEATS IN RELATION TO AGE, AT EACH OF FOUR COLONIC TEMPERATURES
(Data before birth from Goss, 1938, and Burlingame et al., 1942; after birth from Adolph, 1951, and new data.)

when returned to air. But, the time of survival is maximal at about 10° up to 31 days of conceptual age; whereas at ages above 37 days, survival is further restricted by temperature itself, and the longest survival without oxygen moves above the new lethal body temperature of 15°. It may be inferred that various bodily processes demanding oxygen for survival go slower at the lower temperatures, and hence are not so soon exhausted; this is the rule that holds after infancy. But in infancy, temperature also has an effect of its own whereby survival is much shorter at 2° than at 10°. This short survival is scarcely affected by the absence of oxygen before 31 days of age, nor by the fact that heart-beats are suspended at the lower temperature.

Undoubtedly the effects of temperature upon most bodily processes generally change with age. No one known process can be considered to limit survival, and yet many single processes could con-

tribute to the lethal effect. What is apparent is that the *relative* rates of various processes at a given temperature change with age. Some such distortion among rates may account for the change of lethal temperature during the development of the rat. Which particular disproportion becomes lethal cannot now be guessed.

Summary

The serial unfolding of heat-regulatory processes is actually continuous from generation to generation. Maternal care constitutes a regulation A that has no beginning, and ends only with weaning. Regulation B, the tolerance to low body temperatures, tides the infant from birth to the sufficient development of regulation C, when it is lost.

TABLE 1

Days of conceptual age at which each regulatory function of rats matures

Function	Half-Mature	Fully-Mature	Source
Extra heat production	32	47	Fig. 2
Net heat loss	33	44	" 7
Brain capillaries	33	42	" 9
Brain myelin	31	45	" 10
Adrenals △ ascorbate	36	38(?)	" 12
Survival temperature	37	46	" 13

Responses to warm atmospheres are developing in ways parallel with those to cool atmospheres. But no one has ascertained the changes in panting movements or in sprawling posture that come with age; when they can be said to be adult has not been determined. Adult regulations depend in great part upon specific sense organs and synaptic systems which function to promote heat gain or heat loss, in accordance with the actual heat content of the body. Attempts to identify the beginnings of hypothalamic interventions in heat exchanges, for instance, have so far proved inconclusive; the known interventions are progressive, as shown by the studies of structural developments.

The serial unfolding of heat regulation C actually begins long before birth; perhaps even before fertilization. Among the regulatory activities no separation of structure from function can be made; thus, hair is just as instrumental as oxidizing enzymes in the control of heat exchanges. At no sudden time does a non-regulating individual become a regulating one. Also, the entire pattern of regulation is never "complete," for the rat continues to increase its resistance to cold air the larger its body becomes.

Information here presented from which to construct an engineer's blueprint of the heat-regulating system of the developing animal is far from adequate; many researches are needed to fill out the story. What materials we have, however, are sufficient to substantiate our concept that regulations develop gradually and serially.

We can actually estimate the maturity of various regulatory functions. Thus, Figure 2 shows how much extra heat production the infant mobilizes when chilled at each age. At 21 days no extra heat is produced; that is, the metabolic quotient is 1. At 32 days, half as much extra heat is produced as in the mature rat, and at 47 days the same amount of extra heat is produced as in the adult rat. This is the time-table for growth of the control of heat production. In a similar manner we can estimate the degree of maturity of the secretory response to cold in adrenal glands, the relative heat loss, and other factors (Table 1). From these estimates we conclude that heat production and heat loss follow nearly the same schedule, being half-grown at 33 days of conceptual age. Brainstem structures mature at a similar age, while adrenal response and loss of survival of extreme hypothermia are not half-grown until 36 days. According to these partial data, then, full maturity of heat regulation is reached in all respects at 47 days; until then each control marches in its serial order in the procession of development.

Also, at every age a cross section of the constituent factors of control reveals how they together seem to yield the total regulation C. Suppose, for instance, that we compare the several processes of heat regulation at 22 and 42 days of age. To basal heat production is added the extra heat production in response to cold, so that the later metabolic quotient more than doubles (Fig. 2). Concomitantly the ratio of weight to surface doubles, and hair density rises from zero to approach that of adults (Fig. 6). As a result the cooling rate drops 90 per cent, and the air temperature for summit metabolism decreases from 31° to 12°C. (Fig. 5). The adrenal cortex, which at first responds only to ACTH, now responds to epinephrine and to cold air as well. No over-all index has yet been developed to condense all this informa-

tion into a single number. But the controls seem to be interlocked; and the fact that fewer processes participate during infancy than during adulthood allows us to watch their progressive complexing.

Oxygen Regulation

Survival without Oxygen

Tolerance at Birth

Infants are more tolerant of hypoxia than are adults. Is this tolerance parallel to the tolerance of low body temperatures? Have the two tolerances some common basis?

From ancient times it has been known that a viable infant may be extracted from the uterus of a mother that has been dead for some minutes, both in humans and in domestic animals. William Harvey (1651) asked how this could be, and Robert Boyle (1670) experimented on the matter. Newborn kittens were subjected to vacuum, and although breathing and heart-beats ceased for many minutes, some kittens recovered and lived; adults did not. Another critical experiment was devised by Buffon (see Edwards, 1824, p. 167). Buffon placed a bitch in a frame with her rear end under warm water. There she gave birth to three pups, in such manner that the pups did not come in contact with air. After a few minutes the pups were submerged in warm milk "so that they could take nourishment." There they stayed for half an hour; upon withdrawing them to air, all breathed and lived. They respired for half an hour, after which they were again submerged in milk for another half hour, and later for still a third half hour. They survived.

That newborn animals survive long periods of time without air was found in an independent fashion by Legallois (1812, p. 25). He, too, observed a difficult human delivery, which made him want to know low long an infant animal born at term could survive without breathing. He found that infant rabbits continued to move their limbs for the same length of time whether they were strangulated, submersed, or decapitated. But the time of continuance varied with the age. He asphyxiated rabbits of 0, 5, 10, 15, 20, 25 and 30 days of age (1834), and noted that the signs of life persisted for a shorter time in the older animals. In the newborn they lasted 15 minutes; at 30 days of postnatal age they lasted less than 2 minutes.

In rats, various end-points of tolerance may be used during subjection to anoxia or hypoxia. One is the duration of breathing or gasping movements (Fig. 17); the duration decreases greatly in the first ten days after birth. The same relation holds for rats subjected to any limiting pressure of oxygen (Britton and Kline, 1945). Other studies have relied on heart-beats or limb movements. But, as Boyle reported, infant animals may recover after cessation of all movements. Hence it is also desirable to subject infant animals to absence of

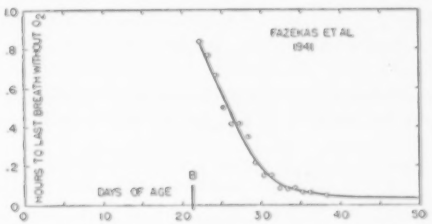

Fig. 17. Duration of Gasping in Infant Rats Suddenly Deprived of Oxygen by Placement in Nitrogen of 24° C.
(Data of Fazekas et al., 1941.)

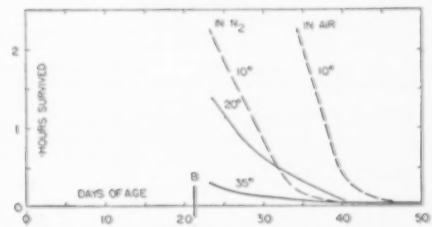

Fig. 18. Times of Deprivation of Oxygen that were Survived (Spontaneous Recovery of Breathing) by Most Infant Rats at the Three Body Temperatures Shown; also Times Survived in Air at the One Body Temperature of 10° C
(Data of Adolph, 1948.)

oxygen for diverse lengths of time, and later to observe whether they recover. Temperature of body and air may also be controlled artificially; if oxygen be removed while animals are in a gas atmosphere, the younger animals cool more than the older, as was seen in Figure 5. Taking all these factors into account, we find (Fig. 18) that the decrease of anoxic survival-time with age can be observed at any one temperature, but the time is greatest at body temperature of 10°C. We also find that at this temperature the times of survival are much longer than those of persistence of gasping movements; in other words, breathing may be

suspended for as long as an hour, being resumed upon the return of oxygen.

The ability to survive without oxygen has, no doubt, a use in many fetuses during the birth process. How it is provided, only to be lost later, needs definite study.

Factors in Tolerance

The following additional facts have been ascertained about survival of newborn rats without oxygen at 25° to 35°: (a) survival may be prolonged somewhat by administering glucose, and shortened by giving insulin (Himwich, 1942; Hicks, 1953); (b) survival may be reduced to near that of adults by giving iodoacetate (1 μmol./kg.); and (c) lesions are produced in many regions of the brains of newborn rats allowed to survive one day after sub-lethal exposures (Hicks, 1953). These three items suggest that biochemical and localized metabolic factors partly limit survival.

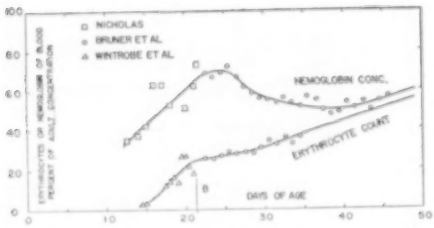

FIG. 19. HEMOGLOBIN CONCENTRATION AND RED BLOOD CELL COUNT OF BLOOD FROM RATS OF VARIOUS AGES

In each case the mean adult value is taken as 100 percent. Squares, data of Nicholas (1928); triangles, data of Wintrobe et al. (1936); circles, data of Bruner et al. (1938).

In order to analyse further the factors that control survival without oxygen, we will make two excursions. One will exhibit the development of the blood and its capacity to transport oxygen; the other will inquire whether the metabolism of the brain can furnish a key to the development of oxygen regulations.

Blood

Composition

Blood furnishes oxygen transport. The hemaglobin in its corpuscles is believed to be indispensable to the maintenance of a warm-blooded body much larger than the ovum. So we now inquire when and with what properties the blood develops. How is it related with the regulation of oxygen in the whole fetus and infant?

When the heart first beats, some red corpuscles are already waiting to be moved, suspended in plasma. The first red corpuscles may be seen at 9 days, forming in the "blood islands." These corpuscles are characterized by large size and by presence of a nucleus.

At first the circulating blood is mostly plasma. The "red blood count" (number of erythrocytes per unit volume of blood) progressively increases throughout fetal life (Fig. 19). So does the hemoglobin concentration, for the amount of hemoglobin in a unit *volume* of corpuscles is approximately constant. But the hemoglobin in a given *number* of cells becomes uniform only after 40 days of age.

Plasma is at first very dilute, having 96 per cent water at birth (Hatai, 1918); indeed the whole fetus is dilute, having 93 per cent water. The most specific constituents of plasma are its several proteins; in adult rats they are produced largely or exclusively in liver (Miller and Bale, 1954). At birth the liver may or may not have attained a stage capable of producing each of them (Dumm, 1943). The concentration of total solutes (Hatai, 1918) and of total protein (Toyama, 1919) in the plasma increases progressively. Thus a liquid that at birth was largely water comes to be a stable and adult plasma. Its volume has not been measured at an age less than 40 days.

Erythrocytes

Half way to birth a transformation of the corpuscles begins. They decrease in volume and in diameter (Fig. 20), and lose their nuclei (Fig. 21). Presence of nuclei is taken as a sign of immaturity in circulating erythrocytes; in adult life the nuclei are lost before the cells leave the bone marrow in which they form. So also the reticulum of the erythrocytes is taken as a mark of partial immaturity; it is still present at the rat's birth in all the circulating cells. Three regulations of fetus evidently differ from those of adults: (a) the cells are added to the circulating fluid as soon as they have acquired their complement of hemoglobin; (b) during their formation they are larger than the erythroblasts that form in later life; and (c) the hemoglobin in these corpuscles differs chemically from the hemoglobin formed after birth (Itano, 1953). The last property is manifested in the molecular conformation of the hemoglobin (Itano);

the conformation has not yet been ascertained for the fetal rat, but is apparent in the dissociation of the oxyhemoglobin (Barker, 1956).

The oxygen-dissociation curve of whole blood has been measured in infants of four mammalian species (man, goat, sheep, and bovine). In all it shows a shift from left to right with age. In several additional species, the oxygen-dissociation curves of oxyhemoglobin solutions have been measured (Barcroft, 1947, ch. 14); they also move from left to right with age. In the infant rat, most of the change with age occurs in the first 12 days after birth (Fig. 22). Evidently the difference in carriage of oxygen depends in part upon the hemoglobin

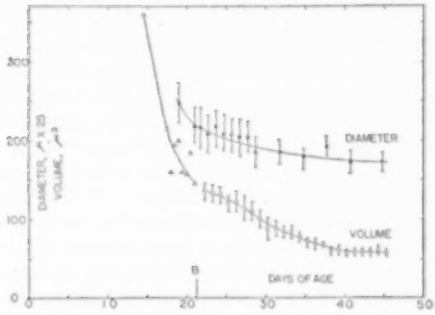

FIG. 20. ERYTHROCYTE DIAMETERS AND VOLUMES IN RATS OF VARIOUS AGES, WITH STANDARD DEVIATIONS

Triangles, data of Wintrobe et al. (1936); open circles, Bruner et al. (1938); closed circles, C. Smith (1932).

itself, whether or not other constituents of the erythrocytes play a part.

The movement of the dissociation curve to the right can be delayed, and even reversed, by intermittent exposure of infant rats to low oxygen pressures (Fig. 22). The difference induced by hypoxic exposure is actually significant at 30 days of age, and probably earlier. Hence we learn that the manufacture of one kind of hemoglobin or another can be steered to a limited extent by an environmental circumstance. At the same time, the concentration of total hemoglobin in the circulating blood is not significantly modified by hypoxia before weaning. Independent controls seem to govern the kind of hemoglobin manufactured and the amount of it.

A specific test of capacity for increase of hemoglobin and erythrocyte production consists in exposing infant rats to a simulated altitude of 25,000 feet (barometer 282 mm. mercury) for one-sixth of each day beginning on the day after birth (Altland and Allen, 1952). Hematocrit ratios in such rats are no greater than in control infants up to 43 days of age. Thereafter marked polycythemia be-

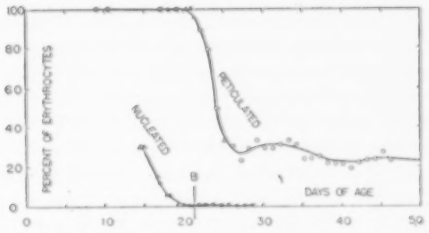

FIG. 21. FRACTION OF CIRCULATING ERYTHROCYTES THAT ARE NUCLEATED OR RETICULATED, AT VARIOUS AGES

Squares, data of Creskoff et al. (1949); circles, Bruner et al. (1938); triangles, Wintrobe et al., 1936 (prenatal) and C. Smith, 1932 (postnatal).

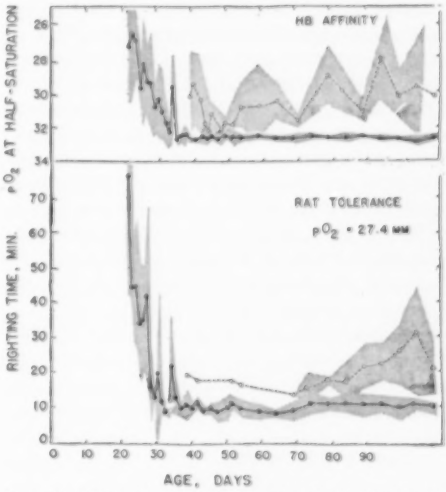

FIG. 22. HEMOGLOBIN AFFINITY AND ACUTE HYPOXIA TOLERANCE AS A FUNCTION OF AGE

(A) in normal rats and (B) in rats after one or more exposures to oxygen tensions of 27–37 mm. Hg for 10–30 min. Solid circles: mean ± S.D. (lined area) in normal rats A. Open circles: mean ± S.D. (dotted area) in the exposed rats B. (From Barker, 1956.)

gins; this marks an adaptation to hypoxia. Similar early absence of blood modifications is also found when exposures are less severe (Contopoulos et al., 1954). This absence suggests that before birth any hypoxia prevailing in the fetal environment does not influence the rate of erythrocyte production. In human fetuses that have suffered severe hypoxia,

however, fetal corpuscles are more plentiful (Walker, 1954). This finding seems inconsistent with the refractory state of the newborn rat; like all inconsistencies, this one calls for more investigation.

Birth marks a crisis in the development of blood. The hemoglobin concentrations of blood and of each erythrocyte decrease, and the fraction of new cells added per day decreases (Fig. 19). Some of the crisis may result from the inadequate mineral content of milk on which the infant rat lives until about 40 days of age. Additional influence may possibly arise from the more complete oxygen supply that follows birth. By 40 days of age the size of the average erythrocyte diminishes to near that of the adult, and the number of red cells per unit volume of blood stands at about half that of the adult.

Does the diminution in erythrocyte size, that begins at 15 days and continues to 40 days, represent a shrinkage of each cell, or a replacement of large cells by small ones? Answers are only partial, for no one has measured the duration of life of fetal cells. In adult rats it appears to be about 60 days (Fryers and Berlin, 1952). The size diminution can be followed in the distributions of cell diameters at diverse ages. These distributions, sometimes known as "Price-Jones curves," show relatively more spread or dissimilarity when the cells are large and are changing rapidly, but all are unimodal distributions (C. Smith, 1932); and there is at present no demonstration that two populations exist. But what of the two or more kinds of hemoglobin molecules? The chances are that they are mixed in diverse proportions in each erythrocyte between early fetus and late infant. The oxyhemoglobin dissociation changes gradually. So, the cells that lose their nuclei while circulating probably last as small cells about as long as cells more recently formed. Only about 55 days after conception has the last of the fetal hemoglobin been replaced from the circulating blood; even this replacement is incomplete if infant rats are meanwhile exposed to hypoxia.

Now we have caught glimpses of the orderly fashion in which blood erythrocytes develop. Every characteristic of their development represents one aspect of regulation. We may distinguish at least four such controlled processes: (*a*) formation of rubriblasts and prorubricytes by mitosis; (*b*) deposition of hemoglobin in the cells; (*c*) movement of cells into circulation; and (*d*) maturation and ageing intrinsic to each cell. Some of the processes, such as the deposition of hemoglobin per unit of cell volume (the cell hemoglobin concentration) are similar from the first cell to the last. Other controlled events, such as the intrinsic changes of size of cells manufactured and circulated, or the type of hemoglobin molecule deposited, vary from fetus to adult. Experiments could be done to find how much of the change with age is commanded by information coming from outside the blood cells. Such are the critical transformations with age in the assembly lines that produce erythrocytes and in the environments that control them.

While we are considering blood cells, one other type of regulatory relation (R) may be mentioned. Such cells represent ideal units for the study of variability. One widespread concept about developing regulations is that fluctuations of a given property are wide in immature animals, narrow in mature ones. Do blood cells vary more at one age than another? An example consists in the standard deviations shown as bars in Figure 20. The bars are taller at early ages than at later; but the means are also diminishing, so that if we divide the deviations by the corresponding means, the resulting coefficients of variation are uniform. Other available data on variabilities among blood cells in the same range of ages yield the same result. This uniformity is not altogether expected, for we might suppose that the transition of cell size in newborn animals would not be synchronous in the whole population. Indeed, the variations evaluated here are interindividual ones, and not intraindividual; so we learn that the individuals are highly synchronized among themselves.

Perhaps we can find other properties in which variability actually diminishes with age. Tolerances to hypoxia as judged by righting times (Fig. 22) show no trend with age in their coefficients of variation. But hemoglobin affinity is much more variable in the first two weeks after birth. However, these weeks are the period during which fetal and adult hemoglobins overlap; and in animals subsequently subjected to high altitude the variability returns. Again we fail to find a clear decrease of variations with maturation of the individual. Probably other instances will turn up eventually, wherein variability will prove to be a function of age; for this demonstration we must choose properties that lend themselves to studies of intraindividual fluctuations.

Relations of Blood to Tolerance

Can we find relations between the blood changes and the whole regulation of oxygen supply in the growing rat? We may look for relations of the following sorts: (a) development of circulatory responses to hypoxia; (b) development of ventilatory responses to hypoxia; (c) rate of energy metabolism; (d) capacity for work; and (e) tolerance to hypoxia and anoxia. Though we examine the significance of blood changes in each of these respects, we need not expect that the blood will prove to be a limiting factor in any one of them.

At present there is little information that bears upon (a) and (b); what exists will be mentioned later. Items (c) and (d) depend in part upon oxygen supply; two things may be said: first, that soon after birth the resting oxygen consumption of the whole individual, and of some of its isolated tissues (Schüler, 1943; Bertalanffy, 1951), is greater (per unit of wet weight) than at any subsequent age; second, that all tissues that have been examined have anaerobic energy metabolism that may conceivably tide them over any temporarily inadequate supply of oxygen. This statement brings us to item (e). Concerning it we have to conclude that the oxygen capacity of blood is well developed long before the tolerance to anoxia is shortened. The oxygen-dissociation curve of the blood is still of the fetal variety, however, and is gradually transforming to the adult state at the very time that hypoxic tolerance is lost. But beyond the synchrony, nothing is known to link the two transformations.

On the whole, our excursion into blood physiology calls attention to an additional host of regulations as they fit into the time schedule of respiratory development. Most of the consequences of this particular fit, as contrasted with some other hypothetical one, are not yet apparent. Granted that oxygen transport is prerequisite to the functioning of most other tissues, of the intrinsic controls over oxygen supply, and of the feed-back from oxygen pressure of arterial blood through arterial chemo-receptors, still the details needed for greater understanding are lacking. In this case we are working from knowledge of the adult to that of the infant; what we hope is also to add to our understanding of the adult from an independent insight into the regulatory physiology of the infant.

Brain

Structure and Composition

Tolerance to anoxia requires that every tissue be capable of surviving without oxygen. Death of an adult animal in asphyxia is never credited to skeletal muscles; they transform energy for long periods of time by anaerobic processes. Some other tissues (kidney, liver) do likewise to small extents. Heart and brain, on the other hand, are ordinarily regarded as limiting the animal's tolerance. If we could find a change in the metabolisn of one of these, coincident with the change in tolerance of the infant rat as a whole, a source of adult intolerance might be located.

Hearts of fetuses and infants continue to beat in absence of oxygen longer than do those of adults. Precise durations have not been recorded for diverse ages. Enzymic changes, or metabolic changes of hearts in vivo, have scarcely been examined. Since infant hearts may beat long after ultimate survival of the whole animal has become impossible due to lack of oxygen, the brain and its parts may rank above the heart as a tissue damaged in anoxic death.

Structural examination of the brain has been especially thorough (Donaldson, 1924). Bulk, sizes of subdivisions, water contents, cell sizes and cell numbers, vascularization, and other features are known. From such information it can be said that development of the whole brain and of the brain stem, relative to the body as a whole, is greatest within a few days after birth (Fig. 8). As cell numbers cease to increase, vascularization and myelinization (Fig. 10) become accelerated. The relation of these to regulatory functions is not yet clear; we are in the same predicament as we were in studying the blood, for all these changes forerun the change of function by so many days that no limiting factor can be recognized as linked to function.

Enzymic Activities

In isolated brain tissue, anaerobic glycolysis is available, and is increasing in intensity postnatally in both pallium and brain stem (Fig. 23). Greater intensity also means that the tissue's own reserves of carbohydrate may not last for so long in older ages. In any case, in vitro glycolysis of brain tissue persists at ages when survival of the individual by anaerobiosis has been lost.

Aerobic metabolism of rat-brain samples has been fractionated, in order to ascertain whether the

increases with age are alike in all fractions (Fig. 24). At birth, little inhibition resulted from treatment with malonate; after 29 days of age, half the respiration was inhibited by it. The part inhibited is generally considered to be paced by succinic dehydrogenase (succinoxidase); evidently the activity of this enzyme system develops almost entirely postnatally. However, again it is difficult

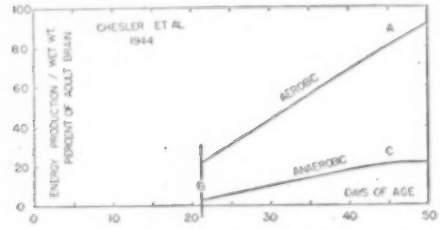

FIG. 23. ENERGY PRODUCED IN BRAIN TISSUE ISOLATED FROM INFANT RATS, AS MEASURED AT DIVERSE AGES BY THE AEROBIC AND THE ANAEROBIC RESPIRATION

Maximal aerobic respiration occurred at 71 days of age and amounted to 0.20 Cal./kg. min. (Data of Chesler and Himwich, 1944.)

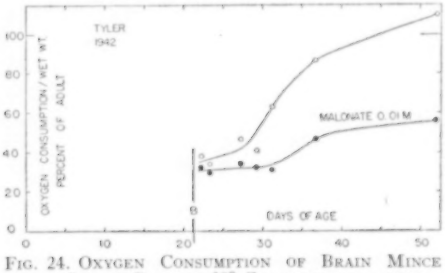

FIG. 24. OXYGEN CONSUMPTION OF BRAIN MINCE FROM INFANT RATS AT 38° C, WITHOUT AND WITH ADDED MALONATE AS INHIBITOR

Adult maximal consumption was 29 ml./kg. min. (Data of Tyler, 1942.)

to see what relation this development bears to the loss of ability to survive without oxygen.

Changes of chemical composition of the brain can be examined (Fig. 11); for instance, phosphocreatine first appears in the rat brain at about 30 days of age. Enzymes active in glycogen synthesis and glycogen hydrolysis become plentiful about 33 days of age. Carbonic anhydrase, choline esterase, and acetyl phosphatase increase in activity from birth onward. Evidently a large number of activities are increasing in the brain at any one age. We naturally focus attention on those that occur most rapidly, such as phosphorolysis. But whether rapid or slow, little correlation can be drawn with the loss of tolerance to anoxia. We are particularly looking for some process that disappears from the armamentarium of brain tissue at the ages when tolerance to anoxia and tolerance to hypothermia disappear. But none of the changes of metabolism or composition that have been reported are prompt decreases; they are all gradual increases. One of these latter, such as phosphoglycomutase in phosphorolysis, could conceivably cover up a part of the anaerobic process, but no such covering-up is known.

In general, the measurements of energy turnover at various ages show that at least some parts of the mature brain have plenty of anaerobic metabolism in vitro (Fig. 23). But something prevents its utilization for survival in vivo. One theory that may represent such a fact states that with age, the oxidative transfer builds up its intensity, after which high intensity is indispensable. Possibly this build-up is signalled by the presence of phosphocreatine at 30 to 35 days of age, where none existed before (Fig. 11). Once this has happened, glycolysis in brain is unavailable, not by non-existence of suitable enzymes, but by the type of system handling the energy transfers. Actually glycogen synthesis and utilization have both been facilitated at this age. In other words, a critical intensity may be reached by the gradually developing processes of energy utilization, which does not inhibit glycolysis as measured in a tissue slice or extract, but which makes low intensity transfers ineffective. In some such way we may harmonize the existence of anaerobic metabolism in vitro with its ultimate ineffectiveness in vivo.

Relation between Tolerance to Anoxia and Tolerance to Hypothermia

Hypoxic Tolerance Test

Tolerance can be tested not only by survival but also by any other measurable end point. A convenient test depends upon loss of righting reflexes as seen in inability to stand. A particular oxygen pressure is chosen to which rats of diverse ages are exposed (Fig. 22). In newborn individuals, righting is long retained. About two weeks later it is reduced to an adult time, and this reduction parallels the movement of oxyhemoglobin dissociation to a new and permanent position. Probably the oxyhemoglobin activity is a factor in the change of this tolerance, whereas it is not a factor in the survival of complete anoxia.

Tolerance time is modified, becoming longer after infant rats are exposed occasionally to low oxgen pressures. At any time of life the prolonged tolerance time can be partially regained after it has been lost (Fig. 22). Thus are revealed two regulations, that which determines the loss of righting and that which determines the adaptation of this loss to another level.

Comparison of Tolerances

Ability to survive anoxia decreases in a manner resembling the ability to survive low body temperatures, both in growing rats and among species. Species in which newborn individuals are intolerant to hypothermia, such as guineapig (Adolph, 1951) are also intolerant to hypoxia (Edwards, 1824) and to hypoglycemia (Himwich et al., 1943) and have regulation of their body temperatures well developed (Pembrey, 1895). Not only qualitatively but quantitatively the two tolerances are strikingly similar. Naturally, it has been supposed that hypothermic death is hypoxic death in infant (e.g., Himwich et al., 1942) as well as in adult. The decision on this notion has to be made partly from studies at a temperature that is survived by the infant but not by the adult. Such a temperature is 10° C. (Fig. 18) and there it is found that the longer survival without oxygen is lost a few days *before* the longer survival of hypothermia. In spite of the general resemblance of the two tolerances, we are forced to conclude that at least a part of the hypothermic tolerance is independent of the hypoxic tolerance (Fig. 25). Indeed, all survival at body temperatures below 10° C has a special character; it is shortened as the temperature falls, instead of being prolonged by cooling as it was above 10° C. At the same time, oxygen prolongs infant life below 10° C., whether the rat is breathing or is not breathing.

There seem to be special differences between tolerance to hypoxia and tolerance to hypothermia. Supply of glucose, and a number of other metabolic factors, prolong tolerance to hypoxia in both adult and infant rats (Britton and Kline, 1945). But none of these factors have been found to modify the tolerance to hypothermia at any age.

How cold tolerance disappears at 40 days of age can only be surmised. Enzymic concepts could be modified in such a way that one of the activities in the brain that has become essential at an age between 35 and 40 days fails to function below 15°. For instance, a temperature below 10° or 15° may paralyse some metabolic process, such as it does in tissue slices; this same process is reversible in the infant if not too much time has elapsed.

The case may be stated thus: hypothermic tolerance is prolonged by the presence of oxygen at all temperatures, and more by pure oxygen than by air. The prolongation does not depend on visible breathing, and artificial breathing has no effect, although in the non-breathing infant, diffusion respiration may contribute something. Further, hypothermia prolongs anoxic tolerance down to 10°, but shortens it below 10°. So the two factors of hypothermia and anoxia interplay. The fact that there is a time factor in survival itself suggests

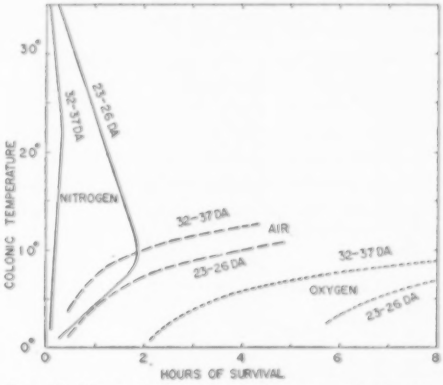

FIG. 25. MEAN DURATIONS OF SURVIVAL (SPONTANEOUS RECOVERY OF BREATHING) OF INFANT RATS HAVING VARIOUS COLONIC TEMPERATURES AT TWO CONCEPTUAL AGES IN THREE KINDS OF ATMOSPHERES (From Adolph, 1948.)

that duration of life is limited by a metabolic factor or factors. Farther than that we cannot proceed at present.

On the whole, we see that high tolerance to anoxia and to hypoxia disappears during infancy. In part a change of metabolic machinery with age accounts for the disappearance. It might be supposed that such a useful tolerance would be retained in adults; we can, if we wish, guess that some price, unknown to us, is too high to pay for its retention.

Survival without oxygen is a regulation B. As in heat regulation, this regulation is available to the infant between the time the supply of oxygen is furnished by the mother through the placenta (regulation A) and the time the infant has developed the complement of self-regulations C that characterize the adult. Regulation B of tolerance

to low oxygen bridges a period of uncertainty in supply during birth and perhaps thereafter.

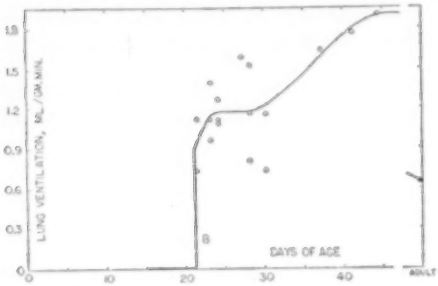

FIG. 26. VENTILATION OF PULMONARY TRACT IN RELATION TO AGE
(New data.)

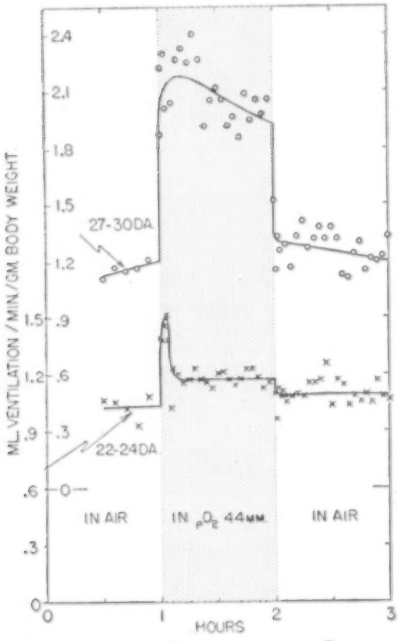

FIG. 27. COURSE OF VENTILATION OF PULMONARY TRACT BEFORE, DURING AND AFTER BREATHING A LOW PRESSURE OF OXYGEN DURING A PERIOD OF 1 HOUR

Each point is the mean of 6 tests on rats of two conceptual ages. (New data.)

Breathing

Normal Breathing

Ventilation of the lungs in infant rats is measured by placing the body in a plethysmograph (volume enclosure), the volume-pressure changes of which are recorded with a strain gauge. A diaphragm at the neck separates the body from the air which is breathed. Body temperature is maintained by enclosing the plethysmograph in an incubator.

In newborn rats the frequency of breathing is highly variable. It averages about 110 breaths per minute, decreasing only after 40 days of age. The tidal volume increases with the size of the body; in this way the ventilation of the lungs (Fig. 26), after 20 days of build-up, keeps pace with the resting oxygen consumption throughout growth. Both ventilation and oxygen consumption per unit of mass diminish gradually with age beyond 40 days, as though tidal volume stays proportional to body mass while frequency slowly decreases with larger size.

Breathing in Hypoxia

When newborn rats are given a low pressure of oxygen to breathe, the ventilation of the lungs increases significantly (Fig. 27). The increase is represented chiefly by increased depth of breathing, for the frequency of breaths changes little. Characteristically, at 22 to 24 days of age, the increased ventilation is not maintained but regresses after a few minutes. A similar phenomenon is found in human infants, and is ascribed to fatigue of some part of the central nervous system when inadequately supplied with oxygen (Cross, 1954).

Infant rats of 27 to 30 days of age respond more markedly to the same low pressure of oxygen. The increased depth of breathing is now maintained for an hour (or more). In these few days the hypoxic response matures.

The frequency of heart-beat usually responds to hypoxia by decreasing in a sustained fashion. At the close of the hypoxia, the frequency suddenly falls somewhat further, and thereafter slowly recovers during half an hour. Apparently the changes of heart frequency during hypoxia do not parallal the changes of breathing.

When hypoxia is removed and the infant rats again breathe air, they sharply decrease the ventilation of the lungs, thereafter returning to the usual depth and frequency. This after-effect shows that there is no oxygen debt, at least none that stimulates more breathing. In no phase does the ventilation rate parallel the heart-beat frequency.

We conclude that newborn rats, like newborns of a number of other species, respond to lack of

oxygen by a moderate increase in ventilation of the lungs. Hence this response is ready sometime before birth. In the fetal sheep it has been traced to the first half of gestation, being first elicitable at 50 days whenever the umbilical cord is experimentally occluded (Barcroft and Karvonen, 1948). In rats born at term, the response to hypoxia is much less on the day of birth than a few days later, suggesting that the breathing reflexes become enlarged, perhaps in recognition of the new life in air.

Chemoreflexes

The adult mammal's responses to hypoxia are mediated predominantly through the chemoreceptors of the large arteries. The carotid chemoreceptors have been shown to be necessary for the so-called anaerobic gasps of infant rats (Tschirgi, 1946). Therefore they are believed to be functioning immediately after birth, and possibly long before birth.

Infant rats respond to anoxia in a way qualitatively different from adults. This response is seen clearly in isolated heads. Cessation of circulation to the head promptly induces gasps; in the infant and adult alike about four are given, and they cease in a few seconds. A second series of anaerobic gasps begins after the first aerobic series has ceased (Selle, 1941). In infants the second series lasts many minutes, in the adult only a few seconds. Their number and duration depend on the temperature of the head and of the surroundings (Cheymol, 1952). The two distinct breathing responses suggest the existence of partially-separate responding systems, about which something can be said.

Tschirgi and Gerard (1947) studied carotid body function at ages up to 48 days, counting gasps after decapitation of the rat, after cyanide, or during oxygen lack, all of which had like influences. They also perfused the carotid region of adults separately from the brain, and found that to obtain anaerobic gasps the anoxia is required in both brain and carotid simultaneously. The gasps are reinforced or potentiated by 35% carbon dioxide, but only when the latter impinges on carotid bodies. The gasps are abolished by iodoacetate, and hence depend upon glycolytic metabolism. The cessation of gasping is not due to lack of motor function or to lack of sensory function, since conduction of nerve impulses could be demonstrated; apparently the earliest failure is in the brain, as we suggested above.

In fetal sheep, something is known of the development of reflex responses to asphyxia as they emanate from the carotid bodies (Barcroft and Karvonen, 1948). Half way through gestation the fetus gasps freely whenever the supply of oxygen is interrupted by pinching the umbilical cord. Thereafter, the response is "inhibited," and is scarcely elicitable until after birth. While the abeyance of the response may save the fetus from more inhalation of amniotic fluid than it otherwise takes into its lungs, it could still be argued that if the response were available, it would be useful in initiation of breathing at emergence from the birth canal.

Thus the anaerobic gasps are largely dependent upon carotid bodies, and these gasps are given by rats just born. The conclusion might be drawn that carotid reflexes become functional just as soon as the infant is free of the mother. Evidently more is to be found out concerning the pattern connected with the first breath of air, for it may somehow make available the gasping response to anoxia that was in abeyance until then. Whether the same chemoreceptors operate to increase the ventilation of the lungs in hypoxic newborn rats is not known.

Tissue Metabolisms

Tissues in Isolation

Every cell transforms energy at rates that are self-controlled in large part. Undoubtedly these controls change with age. Thus, in rat fetuses the available anaerobic metabolism is, in proportion to the aerobic, greater than in later life. However, glycolysis, though present in isolated fetal tissue without oxygen, does not show itself in the presence of usual oxygen consumption (Negelein, 1925), and therefore may not operate in an actual steady state.

The intrinsic control of energy metabolism before birth is little understood. Isolated fetal tissues have been studied with respect to oxygen consumption in sheep (Carlyle, 1948). These tissues have already differentiated the chief metabolic rates and patterns that characterize them in adult animals. During the transition in rat from undifferentiated cleaving ovum (Boell and Nicholas, 1948) to implanted fetus, the distribution of tasks among embryonic parts has not been documented by metabolic observations upon tissues isolated from intermediate stages.

The respiration of tissues from particular regions

of rats has been measured at diverse postnatal ages. Per unit of dry tissue weight, the oxygen consumption is remarkably uniform with age (Schüler, 1943; Bertalanffy et al., 1951). Twelve different tissues are represented in available studies; it will be recalled that all growing tissues are meanwhile gaining in solids per unit of wet weight. The very moderate increases of respiration during early ages that are reported for kidney, thyroid, and testis may or may not be significant ones. In later life some of the tissues definitely diminish their rates of oxygen consumption; these are diaphragm, heart, and liver.

Again, every tissue has a characteristic rate of oxygen consumption. If each tissue and cell has a pacemaker for its energy transformations, age studies may help to identify it or them. Enzymes and substrates are possible ones. Brain is the tissue most thoroughly studied (Fig. 11), but at present we are able to learn little from the array of enzymes in all degrees of maturation that are found in it at diverse ages. Extrinsic controls, such as hormones, may work upon tissues both before and after isolation, but none has been tested at early ages.

Heterogony

For whole animals, diverse functions and structures have proven to be related with body weight by power factors. Since they are related to weight, they are also related by power factors to one another (Adolph, 1949). The "heterogonic" equations that relate them, when applied within the species, show a host of precise interrelationships with body size that steadily increase with age. Most of the functions measured are measured only by rather coarse methods, and for this reason we deal with rats from about 40 days of age and onward. The varieties of functions that have so far been treated heterogonically in rats relate oxygen consumption of body (Kibler and Brody, 1942) and of tissues (Bertalanffy, et al.) with various organ weights (Addis and Gray, 1950), various mineral constituents (Forbes, 1955), diverse lipids (Sinclair, 1930; Sperry, 1955), and some organic constituents (Needham, 1942). Up to the present time, little meaning has been attached to the diverse "partition coefficients" of growth so ascertained, and no enlightening relation has been drawn in the course of later rat development. This kind of study serves, however, to emphasize the interrelations among functions whose magnitudes are fit to live together, and to discourage the designation of any one of them as a probable pacemaker of growth.

Tentatively we can conclude that oxygen regulation proceeds intrinsically until other controls develop between 15 and 40 days of age. Thereafter the basal oxygen consumption settles to a rate that is heterogonically related with many other functions, while the capacity for increase under circumstances such as cold exposure is present but also limited. Heterogonic relations are a system of asymptotes which each property in early development approaches as a limit.

Summary

Regulation of oxygen supply and oxygen consumption changes with age in respect to the following: Time of survival without oxygen decreases with age during 3 weeks after birth. Blood begins to circulate with the first heart-beats; the large, nucleated erythrocytes in it change circumnatally to small, unnucleated ones that lose their reticula. New erythrocytes form with a content of adult hemoglobin instead of fetal hemoglobin. Tolerance to low oxygen diminishes within the same period, and partially independently of tolerance to low body temperature. Brain undergoes many changes of structure, composition, and blood supply; no one of them has been shown to limit its activities or its reflex controls of breathing. Hypoxia stimulates the infant rat to increase the depth of breathing, a little on the day of birth and more on later days. Chemoreflexes are concerned in the responses, particularly in the anaerobic gasping. Oxygen consumptions of isolated tissues are differentiated before birth; in some tissues the consumption diminishes with age. In no case has the change with age been shown to depend upon a particular limiting factor.

We now return to the general scheme of ontogenetic regulations. Regulation A is that furnished by the parents. Some part of the regulation for oxygen is available to the gametes, and more of it is present in the oxygen supply of the placenta and maternal circulation. It ceases suddenly and completely as soon as the umbilical cord is interrupted. Regulation B, the tolerance to hypoxia, is probably maximal shortly before birth, and decreases with age thereafter. Regulation C, the control developed by the new individual, is partly developed before birth: the transport of oxygen to tissues, the enzymic and metabolic patterns of diverse tissues, the chemoreceptors, and the syn-

apses concerned with circulation and breathing. With the first postnatal breath much of the control goes into action. Finishing touches develop later, whose quantitative contributions to the whole regulation of oxygen are only dimly known.

BODY WATER

Water Content

Water content represents one of the characteristic constancies of adult mammals. In studying the ontogeny of this constancy, we once more set for ourselves the problem of finding when and how the controls, that result in the steady state, begin to operate. We may examine several kinds of water exchange; excretion, drinking, and internal transudation. Both the volumes and the concentrations of the exchanging fluids will concern us.

Precise regulation of water content is revealed in the over-all uniformity of the relation of water weight to body weight (Fig. 28). Water does not form a constant fraction of total body substance, however; instead, the two are related by power equations, termed heterogonic. Such equations represent parabolas, $y = ax^k$. For water, a uniform exponent, $k = 0.98$, prevails from 14 days to near birth; a second exponent, $k = 0.95$ or less (Forbes, 1955), from birth to old age. The fraction of water in the body is diminishing progressively from 93% (at 12 days) to 87% (at birth) to 67% (in adulthood) of the body weight (Angulo, 1932). Incidentally, Figure 28 emphasizes the fact that the body substance multiplies much more prenatally than postnatally, since the body starts as a zygote of only 2×10^{-7} gm. The increasing proportion of solids represents, among other changes, an increasing mechanical strength of all tissues; and for muscle, the increases of tensile strength have been measured (Nicholas, 1950).

Before birth, the fetus participates in the mother's regulated pool of water and solutes, on some of the same terms as the mother's own tissues. The pool is protected by the maternal regulatory activities from large fluctuations in volume and in concentration. But the net amount of each substance that the fetus withdraws from the pool through the placenta is not controlled by the mother's side, so far as known. That the control is intrinsic to the fetus seems obvious, but is difficult to prove. The total amounts deposited in fetal tissues are the amounts we measure as gains of body size. They are only small fractions of all the fluids and solutes that osmose and diffuse into and out of these tissues. Such net exchanges need to be measured, however, in order to investigate the central question: by what complex is the amount of fluid controlled that shall be deposited in the young animal's body?

Growth may be viewed, in one of its many aspects, as the accumulation of certain chemical components in specific proportions at a controlled rate. It is generally supposed that the rate of accumulation is determined within each cell; hence two pacemakers of growth are the intrinsic cellular increase and the less intrinsic multiplication of

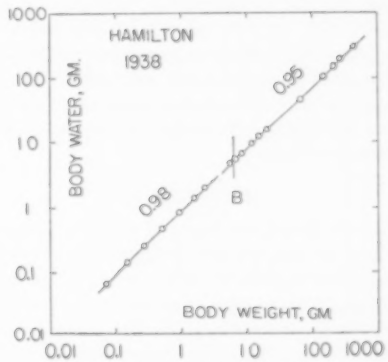

FIG. 28. RELATION OF LOG BODY WATER CONTENT (W) TO LOG BODY WEIGHT (B) IN RATS FROM FETUS TO ADULT

Lines represent the equation $W = a B^k$; values of k are indicated before birth and after birth. Each point represents the arithmetic mean of 5 to 15 analyses reported by Hamilton and Dewar (1938).

cells. The notion that each cell is laying on materials just as fast as it can acquire them is not substantiated; we do not yet know how the total increase of body mass is paced.

For water, or other prominent component of the body, we ordinarily refer the amount present to the total mass of body at each age. But we do not infer that the amount of water is determined by the amount of any one solute component (as in an osmometer), nor by the bulk of a structure (as in a gel).

Chemical Proportions

For various other elementary substances, the heterogonic exponents k of postnatal rats are (Iob and Swanson, 1938; Forbes, 1955):

sodium	0.78–0.85
chloride	0.84
iron	0.67
potassium	1.03–1.14
nitrogen	1.16
phosphorus	1.38
calcium	1.50

Evidently sodium and chloride, which predominate in extracellular fluids, decrease in relative amounts with increase of age; potassium and nitrogen increase. Growth, therefore, is not an accumulation of fixed proportions of substances; all the proportions change with age; and the regulations such as those we are characterizing, unknown in site though they be, are collectively responsible for the proportions. We can go no farther to name pacemakers of accumulation and proportioners of content; so we turn to finding responses to disturbances whereby specific exchanges (intake, output) become activated.

Plan of Study

In our search for ways of characterizing exchanges we can use two approaches to the question of how a prenatal animal regulates its water content. One is to think of an embryo as a mass of protoplasm that succeeds in developing controls largely masked by spatial condensation. The other is to consider the organ processes of the adult as examples of what the fetus also may be using. The first approach has not yet revealed the workings of physiological controls; for this reason we here adopt the second approach, and we will attempt to work backward from what we have learned of adult regulations in order to see at how early an age a mammalian individual can be dissected physiologically.

Here we start with the questions: Are there large differences in control before and after birth? What is the relation of water deposition to excretion?

Certainly the processes of excretion determine in part the amounts of water remaining in the body. In turn, we recognize that, in general, excretion is under the influence of body content or concentration, or both. We first inquire to what extent unusual contents give rise to unusual excretions, in infants as compared to adults. Water is eliminated by two separable paths: evaporation and renal activity. Evaporative losses are found to be similar per unit of body weight in newborn infant and in adult (Heller, 1947), but have not yet been shown to vary with internal water content at any age. We may at once turn, therefore, to examine renal excretion.

Excretion

Methods

The study of excretion depends largely upon our ability to collect urine quantitatively. In the newborn rat the proper collection of urine has proven technically exacting; two methods have been found feasible. (a) The newborn rat does not urinate spontaneously. The mother attends the young by licking the perineal region, which leads reflexly to emptying of the bladder. To a considerable degree this attention can be imitated by stroking the region with a finger or a probe (Falk, 1955). The droplet of urine that then exudes is taken up in a fine glass tube and weighed. Collection periods of one-half to one hour prove reproducible, but only when urine is forming rapidly. (b) A minute plastic tube is placed in the bladder so as to pierce the ventral body wall while the infant rat is under ether anesthesia (Hoy and Adolph, 1956). At a later time, without anesthesia, urine is collected from the plastic tube by fitting a calibrated glass tube to it. The meniscus of urine in the glass tube is read every 3 to 6 minutes, and when the tube is filled another tube replaces it. Urine collections, though small in volume, prove to be amazingly reproducible. The animal is making restrained movements, which help to keep the bladder empty. The urines are available for chemical analysis. In infancy, rats quickly assume a body temperature a degree or two above that of any environment; in order that the temperatures of the infant rats under observation shall be uniform, they are kept in an incubator at 34°. Bladder fistulas usually remain useful for 2 days to one week after they are produced in the first 1 to 5 days of postnatal life. The fistula is usually tolerated by mother rats that have been raised in the laboratory; they accept the young after operation.

Water Diuresis

Any changes in flow of urine in response to a given stimulus are revealed by the course of flow in relation to time. As an example, the effects of administering water by stomach tube are shown (Fig. 29). Flow increases temporarily; the increase is a "diuresis," that is, a significantly greater urine formation that follows after the addition of water to the body.

By what methods shall diverse diureses be

compared? The following seem available:

(a) Magnitude of peak flow.
(b) Time after stimulus at which peak is reached.
(c) Peak flow in ratio to control flow.
(d) Volume output during various elapsed times, as ¼ hr., 1 hr., 2 hrs.
(e) Time required for return in urine of ¼, ½, etc. of the dose of water given.
(f) Duration of flows above a particular rate, as 0.5% or 0.8% of body weight per hour.

All the flows may be reckoned in ml. per hour, or in per cent of body weight per hour, or in ml. per cm.² of estimated body-surface area per hour; some factor related to body size is evidently needed when animals of diverse stages of development are studied. We use the factor of body weight.

Water diuresis may be analyzed into the following phases (Fig. 29): a latent period before diuresis begins, a phase of acceleration of urine flow, and a phase of deceleration of urine flow. Each phase has a characteristic rise or fall and point of inflection. In the infant rat, the latency is greater than in the adult rat, the acceleration is much less, and the deceleration is correspondingly less. The peak of urine flow occurs later in the infant than in the adult. The whole response is miniature and delayed.

Urine forms before birth also, adding itself to the amniotic fluid. Is this urine uniform in rate of formation and composition, or does it vary with circumstances? Wells (1946) and Daly et al. (1947) injected quantities of water and solutions into the rat fetus a few hours before birth was due; at the same time, they tied the urinary papilla so that all subsequent excreta would remain in the bladder until the fetus was delivered by Caesarian section. Water injected into the fetus increases the output above the control output, but not greatly.

In the newborn, the results agree with prenatal ones; water diuresis is small. To persons familiar with the prompt excretion of excess water that occurs in adult animals, the slow and small response in the newborn comes as a surprise, whether seen in dogs (Adolph, 1943) or in rats (Heller, 1947). At this age, urine tends to flow at a uniform rate with a relatively uniform composition. This uniformity may be viewed as a performance refractory to external controls, or as one for which no external controls are available.

The smallness of water diuresis at birth furnishes us a superb opportunity to watch it develop later. Each day of the first week adds to the intensity of response to water excess (Fig. 29). The flow of urine is a different proportion of the water excess at each age; the ratio (clearance) that relates the two is increasing. At present, no evidence has been obtained in rats as to whether birth trips the trigger for development of the response, or whether the same response would materialize at the same age in utero; also whether it develops sooner when birth is premature. In human infants, water diuresis is similarly absent at birth, and develops within a few subsequent days (Ames, 1953). Here the development is equally rapid in prematures; it is triggered by birth.

A characteristic of water diuresis in adults is that by the time the diuresis ceases, an amount of water

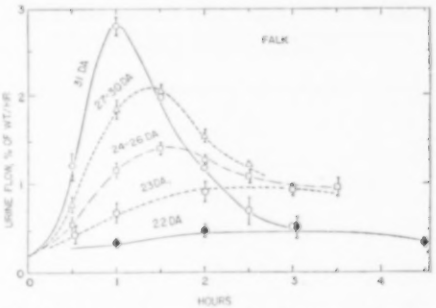

FIG. 29. WATER DIURESIS AT VARIOUS AGES IN INFANT RATS

Each point shows mean and standard error of urine flow at the end of the period of collection. (From Falk, 1955.)

is returned in urine that is approximately the same as the amount placed in the body. In the newborn rat the amount returned is much less than that administered. Much of the excess water resides in the skin (Capek et al., 1956). During the first postnatal days the return increases, and diuresis gradually attains adult proportions, which are reached at 15 to 20 days after birth. At all ages the flow of urine is proportional to the excess of water in the body (Fig. 30); it is the proportionality factor that grows.

Concerning events within the kidneys in diuresis, two views are held: either filtration of fluid in renal capsules is more rapid, or less of the filtered fluid is reabsorbed. Whichever of these views, or both, may be favored depends on future experiments. The other hypotheses about water diuresis deal with ways in which it is aroused. The sensitivity to the blood's dilution or to the increased body-water content could be within the kidneys or

outside the kidneys (as, perhaps, in the neurohypophysis). In the former case, no transmission of influence is required; in the latter case, the kidneys

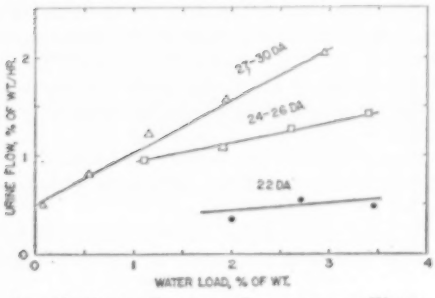

FIG. 30. URINE FLOW IN RELATION TO WATER LOAD OR EXCESS AT EACH INFANT AGE
(Data are taken from Fig. 29.)

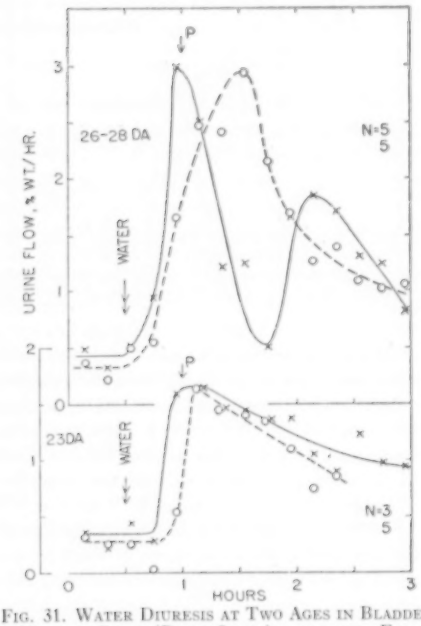

FIG. 31. WATER DIURESIS AT TWO AGES IN BLADDER-FISTULA RATS (DASH LINES), AND THE EFFECT OF PITRESSIN INJECTION AT P UPON IT (SOLID LINES)

(New data.)

may be informed through nerve impulses, or through the withholding of antidiuretic hormone in the neurohypophysis.

Water diuresis apparently may occur without intervention of the antidiuretic hormone of the neurohypophysis. The question is, can water diuresis be prevented by administering an extract of the posterior lobe of the hypophysis? In adult rats it is regularly prevented. In infant rats, tests made by Heller (1952) showed no prevention in the first 30 days postnatally. However, urine collections lasted over 2 hours and evidently were not exact enough to yield a decision. Falk (1955) found prevention at 3 to 8 days postnatally, and it seemed as though all water diuresis could be stopped by the hormone. However, by means of bladder-fistula collections, water diuresis is since found to be very appreciable on the second postnatal day; and on that day, subcutaneous injections of postpituitary hormone (0.1 unit/kg of weight) do not stop it (Fig. 31). Three days later the diuresis, though larger, is prevented temporarily by the same dose of hormone. Even if the urine collections were incomplete, the same difference between these two ages is revealed by the inverse changes of urinary concentrations. From this result it may be inferred that the earliest fraction of water diuresis is aroused through some means other than the temporary witholding of neurohypophysial antidiuretic hormone. This hormone is actually found present in the hypophyses of infant rats 5 days after birth (Dicker and Tyler, 1953), but no search at earlier ages has yielded decisive results. At present, therefore, we cannot tell whether control over hormone manufacture and liberation has been achieved at birth. But we can tell that even if hormone is available, the excretory processes of water diuresis are unaffected by it at two days postnatally. Possibly the renal processes are, instead, directly sensitive to the dilution of the plasma at two days after birth, and perhaps throughout life.

We are now prepared to describe the growth of water diuresis, in terms such as the peak flow of urine (Fig. 32). Before birth, the fastest flow per unit of body weight that can be elicited by water excess is only one-eighth of that in the adult rat. After birth it is similarly small. But in 10 to 15 postnatal days it reached adult dimensions. Tripling the dose of water administered at each age does not change much the growth of the diuresis, although considerably more urine is put out in response to it. Excretory capacity, therefore, is not lacking. We conclude that water diuresis develops in the few days following birth; and that some factor or factors required for diuresis, to be considered later, is lacking at birth.

Epinephrine Diuresis

Absence of water diuresis at birth leads one to the impression that newborn animals are incapable of diuresis in general. Such a broad inference would not be justified without a further test. Is the newborn incapable of diuresis, or merely incapable of responding to a water excess in particular? To find an answer, three other stimuli to diuresis were studied: epinephrine, hypoxia, and salt.

Epinephrine diuresis proves to be available in rats at birth (Hoy and Adolph, 1956). A suitable dose is injected subcutaneously while urine flow is being measured (Fig. 33); within a few minutes, urine flow greatly accelerates, even on the day of birth. A peak flow materializes within a half hour at all ages, which is somewhat greater after the second postnatal day.

Diuresis is similar when an equal dose of nor-epinephrine is given, or when epinephrine is suspended in oil for the injection. In all cases the diuretic urine is dilute urine, making the epinephrine diuresis appear like a water diuresis. But it differs in not being prevented by an injection of postpituitary substance at any age.

Epinephrine diuresis differs also from water diuresis in promptness. Its peak is within the first half hour; the peak of water diuresis is in the second half hour in the late ages, and in the fourth half hour in the early ages (Fig. 29). Evidences are adequate, therefore, to show that epinephrine diuresis differs from water diuresis; indeed, the two are additive.

Epinephrine and nor-epinephrine are present in adrenal glands of rats by the time of birth. Whether they are liberated from the glands at a time when diuresis helps to restore water balance of the individual is not known for any age.

Already it is plain that diuresis can be aroused at birth (and probably before it). Whatever machinery is required for epinephrine diuresis is already available and is presumably the same as that used in the adult. For water diuresis, some portion of the responding units is missing at birth; where that portion might be located is unknown.

Hypoxic Diuresis

Hypoxia induces diuresis in those species of mammals in which it has been adequately tested (man, dog), including rat. If this diuresis can be elicited at birth, then we can reinforce the inference that the failure of water excess to induce diuresis is due to inadequacy of the stimulus itself, and not due to inability of the effectors—that is, the excretory processes—to respond.

Exposure of infant rats for one hour to an atmosphere of 5.8% oxygen (pO_2 = 44 mm. mercury) gives rise to three distinguishable events (Fig. 34). (a) Urine flow is initially inhibited (*oliguria*), often to complete anuria, with minimal flow at 0.2 hour. (b) Flow increases above basal, constituting a *primary* diuresis with peak flow at 0.6 to 1.0 hour. (c) When air (pO_2 = 157 mm. mercury) is restored, a secondary diuresis develops, with peak flow greater than in the primary diuresis, at 0.1 to 0.2 hour of recovery (Hoy and

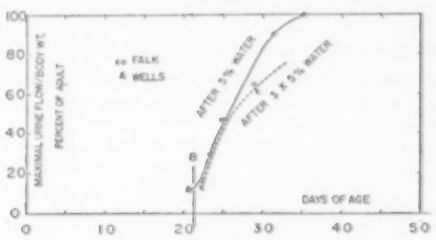

FIG. 32. MAXIMAL URINE FLOW PER UNIT OF BODY WEIGHT DURING TWO INTENSITIES OF WATER DIURESIS IN RATS OF VARIOUS EARLY AGES (Data of Falk, 1955.)

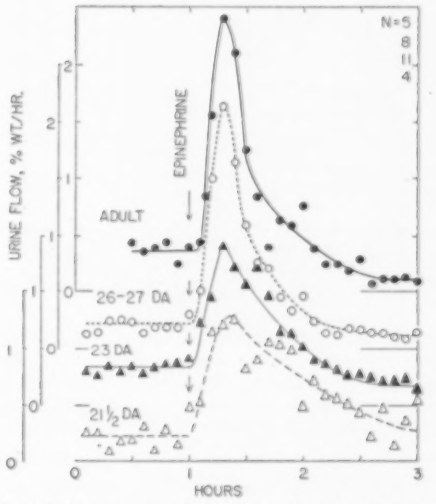

FIG. 33. EPINEPHRINE DIURESIS IN BLADDER-FISTULA RATS OF FOUR AGES BETWEEN BIRTH AND MATURITY
Each point is the arithmetic mean of the tests N in number. (From Hoy and Adolph, 1956.)

Adolph, 1956). These are three phases of hypoxic response.

Infant rats studied only 6 hours after birth show both primary and secondary diureses. The younger animals tend to prolong the initial oliguria, while the same or other individuals 5 days later show the primary diuresis more prominently. Perhaps, then, two influences contend for control of urine flow, one to augment it and the other to inhibit it. At all infant ages, anuria occurs in more than half of the individuals tested.

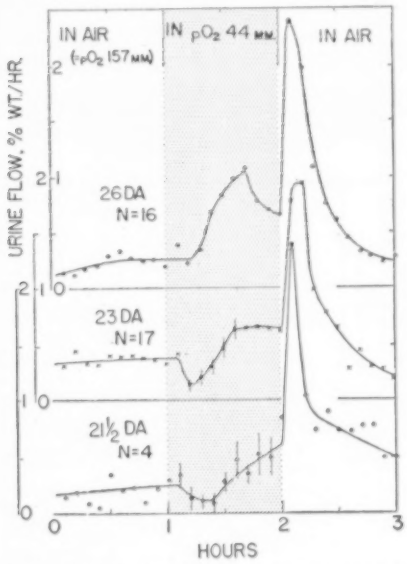

FIG. 34. OLIGURIA AND DIURESIS DURING AND AFTER SUBJECTION TO HYPOXIA IN INFANT RATS OF THREE AGES

At some points standard errors of means are indicated. (From Hoy and Adolph, 1956.)

When hypoxia prevails for only ¼ hour, anuria or oliguria lasts that long, so that upon cessation of hypoxia, it is followed directly by secondary diuresis without any intervening primary one. Hence the secondary diuresis is independent of the primary diuresis evoked during the hypoxia. Its peak is always brief and high. Further, an ensuing administration of low oxygen cuts short the secondary diuresis; this feature illustrates the positive character of the oliguria.

The amounts of urine excreted during an hour of hypoxia are well above control amounts in the early ages (0.3 to 0.5% of weight), are greater at 6 days postnatal (0.6 to 1.0% of weight), and are still greater in adult rat. The minimal flows at the trough of oliguria progress from a mean of 0.08% per hour at ¼ day of age to a mean of 0.23% per hour ($P = .09$). The diuretic flow at 0.6 hour progresses from 0.5% per hour to 1.0% per hour ($P = .01$). Apparently the primary diuresis is still undergoing development in intensity, and whether it is less just before birth than it is at ¼ day after birth we do not know. Altogether the hypoxia for 1 hour leads to an extra expenditure of body water of 0.4 to 0.7% of body weight. The secondary diuresis spends water equal to another 0.6 to 1.2% of weight; it is maximally developed at birth, for it is no greater at 5 days after birth than on the day of birth.

Since secondary diuresis is bigger than the primary diuresis, an infant rat exposed to two periods of ¼ hour each of hypoxia within one hour loses more water in urine than it loses during a single period lasting 1 hour *or* during a recovery period of 1 hour that includes the secondary diuresis. Or, two secondary diureses are more extensive than one. The secondary diuresis is the more prompt and sudden in onset of all diureses tested on infant rats. The only known way to produce diuresis of equal suddenness is to give an injection of epinephrine; water diuresis does not equal it.

How hypoxia influences urine flow has been variously hypothesized in adult mammals. Four views may be mentioned, of which more than one might correspond to phenomena represented in the triple course of hypoxic diuresis. (*a*) Autonomic reflexes to kidney blood vessels. (*b*) Epinephrine secretion reflexly aroused; possibly both *a* and *b* arise in chemoreceptors and modify renal filtration. (*c*) Respiratory alkalosis from altitude hyperpnea. (*d*) Stimulation of neuro-hypophysis resulting in withholding of antidiuretic hormone; both *c* and *d* influence renal reabsorption. Partial decision has been reached in adult mammals (dog, Toth, 1940; rabbit, Franklin et al., 1951) in that hypoxic oliguria appears to depend on sympathetic innervation of kidneys. But in frogs, sympathetic denervation of kidneys did not prevent the total constriction of renal afferent aterioles and the cessation of urine formation in response to hypoxia (Adolph, 1935); and recovery depended upon delivery of oxygen to the kidneys themselves.

In infants, *c* is probably ruled out by the fact that urine remains acid to pH indicators. Hypoxic diuresis is not a solute diuresis, for the urine is

dilute in respect to chloride or to refractive index. Further, it seems doubtful whether antidiuretic hormone in *d* could turn diuresis on and off with the rapidity here observed. Factor *b* (epinephrine secretion) could imitate the single and sharp diuresis with which the adult rat responds to hypoxia more closely than it could imitate any of the phases of infant hypoxic response. Comparing the time course of diuresis with the time course of pulmonary ventilation as described above, we note that sudden increase of breathing accompanies oliguria when hypoxia first supervenes, and also that sudden decrease of breathing accompanies the onset of secondary diuresis. No further details, however, seem to relate breathing and diuresis; in fact, the oliguria does not materialize uniformly at ages when the increase of breathing does. Nothing is parallel between Figures 29 and 34. Hormonal mediators can be imagined that could signal both responses; nervous mediators might equally be operative. The secondary diuresis is effective longer than the decreased breathing of the recovery phase. On the other hand, additional data show that changes of pulse rate last about as long as the secondary diuresis lasts. Still more functions must be measured in the search for parallelisms and common factors.

If we judge from previous experience with hypoxic effects in frog and dog, a tenable guess would be that oliguria is connected with constriction of renal afferent arterioles (factor *a*), as actually seen in frogs when epinephrine or low oxygen is given. Primary diuresis may thus represent increased filtration related to rise of arterial pressure. Primary diureses are commonly seen in unanesthetized man and dog. Secondary diuresis may represent a local vasodilatation (reactive hyperemia) with temporary increase in filtration. Secondary diureses are sometimes observed in frog, rabbit, and dog.

Since all three phases of hypoxic diuresis are available at birth, it may be that they are generally inseparable from one another. Adrenalectomy did not prevent the secondary diuresis from appearing, but reduced its amount. Other interferences might be tested further by partial blocking or cutting of nerves. Current observations indicate that there is no regular succession of oliguria and diuresis in adult animals; that influences are additive so that the strongest prevail (Toth, 1940; Stickney et al., 1946; Silvette, 1943; Franklin et al., 1951).

We conclude that the diuretic responses to hypoxia are more diverse and complicated in newborn rats than in adult animals. Supposition that one or more phases of response to hypoxia would be lacking in infants proves groundless. The whole set of responses is already present at birth; if there is any stage of development at which they are incomplete, that stage is chiefly prenatal. There is also a progression in the size of the primary diuresis in the first few days after birth. The secondary diuresis alone is fully available at birth.

Salt Diuresis

Sodium chloride produces a diuresis, generally classified as a solute or osmotic diuresis. When 0.5 *M* salt is placed in the stomach through a tube, infants of 27 days' conceptual age show gradual increase of urine flow with peak at the fifth hour. Adults show peak flow in the second hour (Falk, 1955). This diuresis changes with age more slowly than those diureses considered above, for even at 43 days' conceptual age it lags behind the diuresis of adult rats.

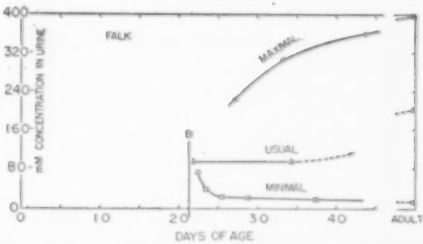

FIG. 35. CONCENTRATION OF CHLORIDE IN URINE COLLECTED FROM RATS OF VARIOUS AGES
Maximal after 0.5 M NaCl solution was given by stomach, minimal after water. (Data of Falk, 1955.)

With or without diuresis, the concentrations of chloride (and total solutes) in the urine of newborn rats tend to be fixed (Fig. 35). This fixity is a sensitive measure of immaturity in excretion. Further, while water diuresis becomes highly developed in about five postnatal days, the ability to excrete excessive chloride develops more slowly. But both dilution and concentration are well developed by the time weaning (at 40 to 43 days of age) lays the individual open to variety in its intakes. Presumably the limitation upon concentrations is in the reabsorptive processes of the kidneys. If the theoretical work necessary for maximal excretion of excess chloride be computed (Fig. 36), it is seen that the development of osmotic work capacity is gradual. But at an age (35 days) when

the work intensity is half developed, water diuresis has reached ¾ of its maximum, while salt diuresis (Fig. 37) has attained only ⅓ of its maximum.

We thus arrive at the conclusion that osmotic diuresis as stimulated by alimentary sodium chloride is slow, and the urine produced is much less concentrated in infant rats. Maturation of the response does not occur in early infancy when water diuresis is catching up with epinephrine diuresis, but at a later age.

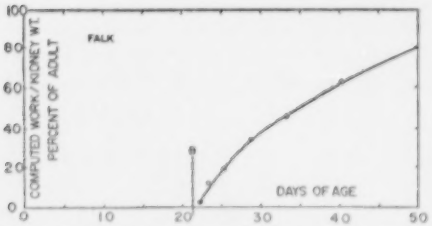

FIG. 36. MAXIMAL WORK INTENSITY IN THE EXCRETION OF CHLORIDE DURING WATER DIURESIS
(Data of Falk, 1955.)

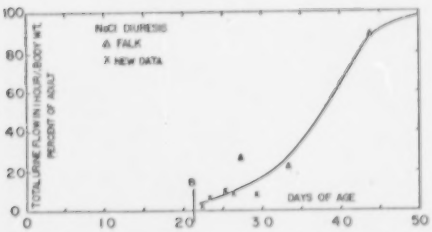

FIG. 37. INITIAL DIURESIS AFTER 5% OF WEIGHT OF 0.5 M NaCl SOLUTION WAS GIVEN BY STOMACH TUBE AT VARIOUS AGES
Triangles, means found by Falk (1955). Crosses, single tests done in bladder-fistula rats (new data).

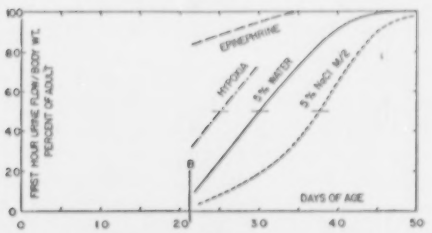

FIG. 38. COURSES OF DEVELOPMENT OF FOUR TYPES OF DIURESIS IN RATS
(From Hoy and Adolph, 1956.)

Comparison of Diureses

When the four kinds of diuresis are compared upon a common time scale, it is evident that maturation is not simultaneous in any two of them (Fig. 38). First one, then another, rises to its maximum, in serial order: epinephrine, hypoxia, water, salt. Whether we can consider this order as one of prerequisite development has not been ascertained, but the serial order suggests a succession of maturations. The succession may not be in the final effector (which might be some one renal process), for diuresis of epinephrine can be elicited even at birth. More likely, some sensitivity or mediator is lacking toward each of the other stimuli. However, we found that the newborn rat's breathing is sensitive to hypoxia even on the day of birth when its excretion is less sensitive. Therefore mediators or transmitters may be the missing elements in response.

In the study of diureses in infant animals, we have considered possible intermediaries and pathways concerned in securing each response. We hoped to find whether the intermediaries were similar in diureses aroused by several agents, such as water, hypoxia, epinephrine, and sodium chloride. And actually we have found that, at birth, the several diuretic responses are in different stages of development. Hence either triggers or intermediaries are distinct. This means that diuresis, even when it produces dilution of urine, is not of one sort but of several.

Were we to limit ourselves to intermediaries and mechanisms, we would miss a particular lesson in physiology, which is this: diuresis is a means by which the composition of the body and its fluids is restored and maintained. It is often a response to excesses. It is one of the processes that result in restoration of body water and solutes after disturbances. We find that some kinds of diureses are ready at birth, as the epinephrine; others are absent at birth, as the salt diuresis. We conclude that at birth the kidneys and blood vessels can produce diuresis. Since, however, they do not do so in response to water or to salt, we may state that this stimulus and the sensations that it produces are not yet linked to the effector system that accomplishes diuresis. Meanwhile the infant is perfectly viable; it is deficient and slow as compared with the adult in its speed of compensation for body excesses of water or salt. The growing rat does not mature in all responsivities in parallel. When one response matures before another, the order of

the series represents an innate priority among the various regulations. Presumably the serial order is, in the main, determined genetically; as ever, the physiological processes appear to unfold. While we are fortunate enough to find some few simultaneous unfoldings that seem linked to mutual controls, for the present we mostly have to be content to make out the time-table in operation.

Blood-Circulatory Factors

Development

If we continue to use current concepts of how adult excretion occurs as our models of infant excretion, we will inquire what is known of various processes in circulation, blood, and kidneys, that participate in excretion. We may be further driven to consider endocrine activities and paths other than renal ones that exchange fluids of the animal body.

The circulation is perhaps the functioning system earliest recognizable in the fetus. Development to effective function involves not merely tissue and organ structures, but also responses of heart and blood vessels through nervous and other influences.

Frequency of heart-beats has been measured, starting from the first cardiac contractions. A biologist feels a thrill at seeing the first heart-beat of an individual. To see it, he should be watching when a rat fetus attains the postconceptual age of 9.6 ± 0.1 days, according to Goss (1938). He might suppose the beats would begin in scattered and gradual fashion, but Goss tells us the rhythm is immediately set at 37 to 42 beats per minute. Thereafter the frequency gradually increases during the succeeding days (Fig. 39). At birth, the infant kept at 37° body temperature has heart-beats of less frequency than those three weeks later, when the maximal frequency is reached.

The arterial pressure (Fig. 39) is exceedingly small during fetal life. There is no sudden change in it when the cardiac valves begin to function. At birth it still is only one-tenth of the adult's mean arterial pressure. The climb is found to be gradual throughout infancy and adolescence. No analysis has been made of the several mechanical factors that determine the pressure at early ages.

The flow of blood depends upon structural developments as well as upon functional modifications, both in heart and in blood vessels generally. Vascularity is increasing in all tissues, as quantitatively illustrated in diverse portions of the brain in which capillary lengths have been measured (Fig. 9). While the channels which contain blood are increasing in extent, nothing is known of their volume contents and their resistance to flow. Factors that pace and determine the enlargement of these vessels are also unknown: it is often supposed that low oxygen pressures in tissues serve to stimulate the formation of more vessels.

The heart increases in weight progressively, but relative to the body its maximal volume is reached a few days after birth. No clear relation can be established between heart weight and the height of arterial pressure.

Chemically, the heart undergoes progressive changes, which have been studied only sketchily. At birth the heart is well endowed with glycogen (Hicks, 1953), which is visibly depleted by brief

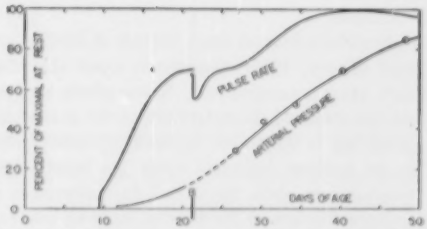

FIG. 39. COURSES OF DEVELOPMENT OF PULSE RATE AND SYSTOLIC ARTERIAL PRESSURE IN RATS

Pulse rates from Fig. 16; arterial pressures prenatal from Burlingame et al. (1942), postnatal from Litchfield (new data). For data on older rats, see Heymann (1949) and Beznak (1954).

anoxia; the depletion is partially prevented by simultaneous administration of insulin. The development of an enzyme is shown by the heart's content of cytochrome oxidase (Kunkel, 1952). Between 26 and 41 days postconception, the specific activity almost doubles; not before 55 days is the activity equal to that of adult hearts. This enzymic activity is one of many that might or might not parallel the low arterial pressure characteristic of the heart before this age.

One enzymic system in rat heart that sharply increases in concentration with age is succinoxidase (Sippel, 1954). Whether its concentration be based on total nitrogen content or on wet weight of ventricles, the enzymic activity parallels the frequency of heart-beats. What connection there may be between enzyme and frequency can only be surmised, since the chemical activities of the minute pacemaker may be more important than those in the whole contracting tissue. Along with succinoxi-

dase activity go increases of number and size of mitochondria (Goss, 1942) to which most of this enzyme is attached. Even in the pacemaker, many constituents are probably becoming relatively abundant during growth, and no one of them may be credited yet with a key position in the tissue's function.

Controls

Extrinsic regulatory influences upon the developing circulation are partially matured before birth. Corey (1935) showed in fetuses of 20 days that the heart increases its rate of beating when the cervical sympathetic nerves are stimulated. Correspondingly, the rate slows when the vagal parasympathetic nerves are excited. But before birth no amount of vagal excitation serves to stop the beats completely; five days afterward cessation of beats is obtained.

Chemical influences upon the rate of beating are found (Corey, 1935); pilocarpine slows the fetal heart, atropin accelerates it. These effects suggest that the chemical characteristics of the autonomic system are in operation. In contrast, epinephrine has no uniform influence upon the heart's frequency before birth, but 5 to 7 days afterward it regularly accelerates the beat. It may be inferred that earlier the heart's pacemaker is not susceptible to the influence of epinephrine, even though a sympathetic influence can materialize. Also it may be noted that epinephrine induces diuresis at an age when it has no influence upon the heart.

The above effects upon the heart may be thought of as "motor excitations" and "synaptic blockings." Ordinarily such end effects are aroused not in motor elements but in receptor organs, and nerve impulses are transmitted thence to the nervous or hormonal motor elements. In adults, the pressoreceptors and chemoreceptors of the arterial system are prominent. When they begin to function has not been investigated in rats. In rabbits, the pressor reflexes seem to be available at birth but do not go into action until the arterial pressure has attained a level high enough to stimulate them (Bauer, 1939). In sheep, the chemoreceptors are similarly functional long before birth but may not be used until birth (Barcroft and Karvonen, 1948). Two sample influences, hypoxia and hypothermia, may work through such receptors.

Hypoxia was tested prenatally for influence upon frequency of heart-beats (Corey, 1935). Neither pinching of umbilical cord, nor closure of maternal trachea, nor maternal hemorrhage led to consistent change of fetal heart rate. But all produced irregular rhythms, which could also be induced by placing lactic acid on the heart or in the maternal blood. At a few days after birth, hypoxia accelerates the heart; it generally slows the heart on the day of birth. It actually deepens the breathing on the very day of birth. Presumably these effects are not mediated through the adrenal gland at this early age.

Influences of hypothermia were compared postnatally in the isolated heart and in the intact heart (Adolph, 1951). At temperatures above 20° C, the intact heart beats faster than the isolated one, suggesting that in the body, regulatory controls are continually exerted upon it. At 29 days the intact heart came to beat still faster than at lesser ages. At about 41 days of age, the ability to beat at all below 9° C. was lost in the intact heart but not in the isolated one. Moreover, for the isolated heart there was no change in rate with age, suggesting that all the postnatal changes found in intact hearts were extrinsic regulatory ones, since they occurred only when the heart was under mechanical, nervous, and chemical influences.

The coordinated development of the rat's circulation is roughly this. Automatic heart beat is initiated at a time when few blood vessels have developed. Slowly more vessels are added, arterial pressure increases, blood fills the vessels, and some controls are operating. Autonomic nervous controls are present before birth, epinephrine control is available at 27 days postconception or earlier; some reflex controls are added thereafter. At no one stage does the fully-coordinated system spring into existence; it develops gradually.

These are the controlling influences that play upon the vascular system as a whole. How they concern in detail the renal blood vessels cannot yet be defined, except as these vessels share the influences that impinge upon all other vessels. With regard to renal function as a whole, it is probable that urine forms only when a renal blood flow or a filtration pressure of certain magnitude is available. That pressure is surprisingly low. At birth it is no greater than 14 mm. of mercury (Fig. 39), and if the colloid osmotic pressure of plasma be subtracted therefrom (about half that of adult rat plasma, Fig. 40) there are no more than 5 mm. of pressure available for filtration. No wonder that urine formation is slow compared to adult. Perhaps

epinephrine in the circulation can augment the filtration pressure, yet it has not been found to augment arterial pressure at an early age. The usual pressure in the arterial system probably increases very little in the next 10 days, while the capacity for urine formation during diuresis increases enormously. How urine can form so rapidly, with such a small filtration pressure, taxes the imagination of those who believe that excess of filtration is the chief factor in diuresis, especially in light of the small expanse of the kidney's surfaces, to the examination of which we now turn.

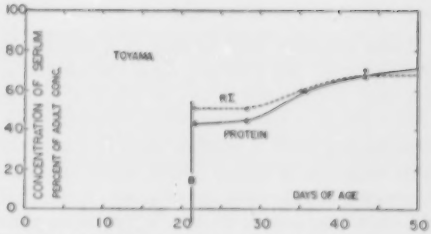

FIG. 40. TWO MEASURES OF SERUM CONCENTRATION R I = refractive index above the index of distilled water; protein = weight of precipitatable protein. (Data of Toyama, 1919.)

Renal Structures and Activities

Kidney Sizes

The kidneys constitute nearly as large a proportion of the body mass at birth as in later life. Maximal ratio between them prevails between 26 and 51 days of age (Fig. 41), after which the ratio slowly declines. Though at birth the whole kidneys are massive in bulk, both on wet-weight and dry-weight bases (Lowrey, 1913), the Bowman's capsular structures are less in size and in number than in adult life (Figs. 42 and 43). The small volume of each glomerulus (one-eighth of adult) means few capillaries in it and a small surface area. The capsule surrounding each glomerulus is thick, and conceivably might retard the translocation of fluid. But the volume continues to be small until 40 days of age, by which time diureses have matured. The number of glomeruli, in contrast, is increasing steadily during the circumnatal period. Glomeruli may be seen in all stages of development, the "immature" glomeruli being partly segregated at the outer surface of each kidney. Those labelled immature are probably not functioning, and many others may not be. From the sizes and numbers of glomeruli one may estimate that only 5 per cent as much capsular surface is available to the newborn as is available to the adult. But again, the surface does not even double by the time diuresis is fully unfolded.

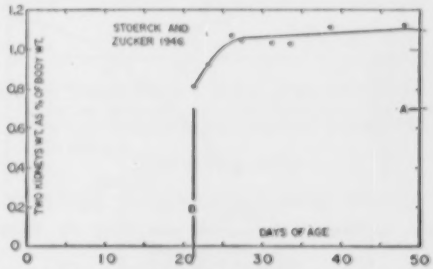

FIG. 41. WEIGHT OF KIDNEYS RELATIVE TO WEIGHT OF BODY FROM BIRTH B TO ADULTHOOD A (Data of Stoerck and Zucker, 1946.)

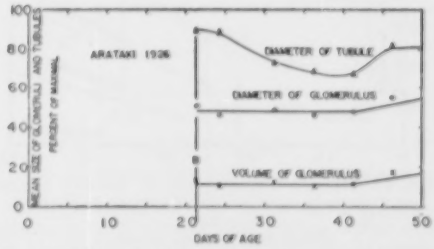

FIG. 42. MEAN SIZES OF TUBULES AND GLOMERULI IN RAT KIDNEYS RELATIVE TO THOSE IN ADULTS (Data of Arataki, 1926.)

Cells of renal tubules vary in volume surprisingly little with age (Covell, 1926). Their nuclei are slightly larger in proportion in infancy than they are in adulthood. The volume of chromosomes in each cell is small at 20 days and increases suddenly at birth (Biesele, 1946). The significance of this event is not apparent; it is mentioned because it is the only renal change that is known to be sudden at that age.

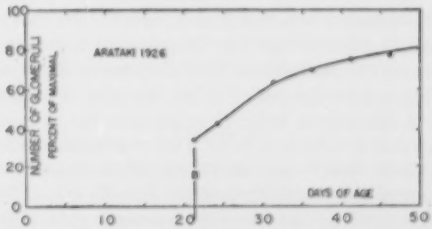

FIG. 43. COUNTS OF GLOMERULI IN KIDNEYS OF RATS (Data of Arataki, 1926.)

Clearances

Inulin clearance may be used as a measure of renal function, and if we rely upon the interpretation that is commonly given to this clearance in adult animals, it may indicate renal filtration flow. Whether expressed in absolute units or relative to body weight or to kidney weight, inulin clearance increases gradually with age (Fig. 44). It is half of the adult clearance at 30 days of age, being most similar to water diuresis in development. But it increases at a slower pace than do any of the four diureses measured; hence it is difficult to believe

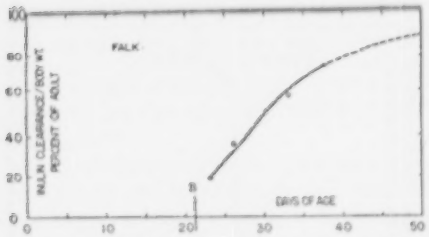

FIG. 44. INULIN CLEARANCE PER UNIT OF BODY WEIGHT IN RATS
(Data of Falk, 1955.)

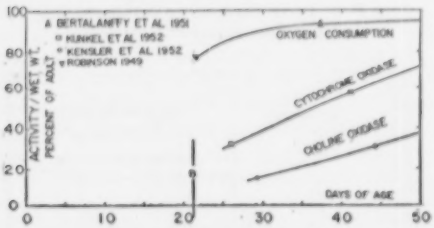

FIG. 45. OXYGEN CONSUMPTION OF KIDNEY SLICES AND CONCENTRATION OF TWO ENZYMES IN KIDNEYS OF RATS
(Data from sources named.)

that the activity it measures is a limiting one for diuresis.

For comparison with inulin clearance, phenol red clearance was measured (Litchfield, new data). At 24 days of age the clearances of both substances are only 10 to 15% of those at 50 days. Throughout this period of life, the ratio of phenol red clearance to inulin clearance does not change; its steady value is 1.65. As in other animals, a ratio greater than 1 can be interpreted to mean that phenol red is actively secreted into the urine. We can conclude that various clearances grow with age proportionately to one another; what their common basis may be cannot yet be named.

A corollary of these facts is that filtration is not the only renal process operating before birth. The fetal urine differs from a filtrate of plasma; hence water and some specific solutes are individually reabsorbed from a hypothetical filtrate. There is no direct evidence that tubular secretion can occur before birth, although Gersh (1937) furnished histological evidence that phenol red might be secreted by renal tubules of rabbit and other fetuses.

Biochemical changes within the kidneys themselves have been little studied; we might hope that a key enzymic activity or substance would suddenly appear at a critical stage of development. Cytochrome oxidase and choline oxidase activities are found to increase gradually (Fig. 45). Oxygen consumption of sliced kidney tissue is almost as high in the infant as in the adult. In fact, the biochemical traits that have been measured are all developing slowly. While many changes are yet unmeasured, it may be that some combination among constituents is required to bring an excretory process to its full capacity, and that no one constituent limits it. Possibly all the building blocks are present but are distributed in less orderly fashion at an early age than later in life. In any case, biochemical steps that limit excretion at birth are as yet unidentified.

We conclude that no single known structure or constitution of the kidneys steps into working order at the particular age at which diuresis matures.

Extrinsic Controls

Regulatory controls from outside the kidneys can be effective at birth, since copious diuresis occurs if epinephrine is administered. The adrenal glands already contain a supply of epinephrine and nor-epinephrine. Subsequently other diureses also develop, particularly water diuresis. Possibly all diureses act by some elementary means such as raising the low arterial blood pressure, but if so the mediations whereby the pressure rises are still immature. Or, it may equally be that each kind of diuresis is much more specific.

Nicotine and pitressin definitely inhibit water diuresis at 24 days of age (Fig. 46). Just before that age they are without influence. Nicotine may have its effect through the liberation of antidiuretic hormone from the rat's own pituitary gland (Burn et al., 1945). At the age at which water diuresis first appears (22 days), antidiuretic hormone (ADH) of the pituitary cannot inhibit it. Two days later,

it can; also at that age the gland can liberate ADH in response to nicotine. These facts strongly suggest that responses of the post pituitary gland are parts of water diuresis, as has often been supposed; but not indispensable parts. Whether that gland is secreting ADH continuously, and even in infancy, has not been directly ascertained. Small concentrations of ADH have been found present in the glands of newborn rats (Heller, 1947).

Our examination of the structural and functional provisions of the circulatory system and of the renal system revealed that materials and activities accumulate postnatally. The hormone study has shown some controls that appear rather suddenly. These controls become effective postnatally, however, at a time when the excretory response to water excesses is already established. Very possibly the presence of the diuretic responses prenatally would have disadvantages. An experiment to test this point consists in injecting large volumes of fluid into nephrectomized pregnant rabbits (Wolff, 1904, 1909). The fetuses are found to take over the task of excreting the excess fluid, suggesting that even slow water diuresis in utero might crowd the amniotic cavity and sometimes produce abortion.

Whatever be the missing links in the newborn's uses of diuresis, or the many deficiencies in renal structure or in hormone formation, it is plain that the last physiological deficiency is overcome within a few days after birth, so that the regulations of water and solute excretions mature, in spite of remaining shortages of renal surfaces and biochemical activities. Thus we see an excretory system—which at birth scarcely responds to circumstances—spring into responsive action within a few days. Probably the event of birth determines when diuresis will mature.

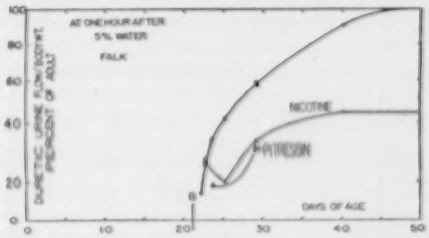

FIG. 46. URINE FLOW 1 HOUR AFTER WATER WAS GIVEN BY STOMACH, AND THE REDUCTION OF THIS FLOW BY PITRESSIN OR NICOTINE GIVEN SUBCUTANEOUSLY

(Data of Falk, 1955.)

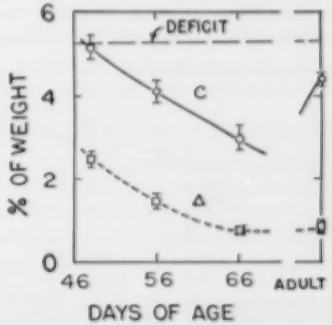

FIG. 47. WATER DRINKING BY WEANLING AND ADULT RATS

Uniform deficits of body weight were created by denying water to the rats; then drinking was allowed for 15 minutes (C) or else water equal to the deficits was placed in the stomach just before drinking (Δ). (From Adolph et al., 1954.)

Water Intakes

Drinking

When we now turn from water output to water intake, we find surprisingly little information available. In our laboratory we observed that newborn dog and rat pups do not drink water in response to water deficit; the newborn infant will drink milk but regularly refuses water. Ten days later the thirst response is developing. Before weaning, about 45 days postconception, the amount of water drunk is more accurately related to the water deficit, as indicated by the fact that at weaning, distention of the stomach by the water drunk comes to inhibit further drinking (Fig. 47). Moreover, after water privation, less of the weight deficit is restored by voluntary drinking at age 65 days than either before or after; the shift of regulation that produces this change has not been identified. Overt behavior suitable to acquiring water to drink develops as a part of weaning, and thereupon the individual's independence in regulating water content is achieved. Before then, the animal in its stages short of independence shows us what living is like without adequate regulations even for water.

Absorption

Absorption of ingested water is slower than in adult rats (Fig. 48). This fact may reflect slower circulation of blood, or other functions, or of both, rather independent of the actual processes that move fluid from the intestine. Absorption does not,

at any age, limit the speed of diuresis that follows administration of water by stomach. It approaches adult dimensions only after water diuresis has matured. The intimate processes of water-electrolyte or nutrient absorption, which probably include some energy-using ones, have yet to be studied during development. When glucose is placed in the stomach, it is absorbed just as rapidly by the newborn as by the adult (Jones, 1951).

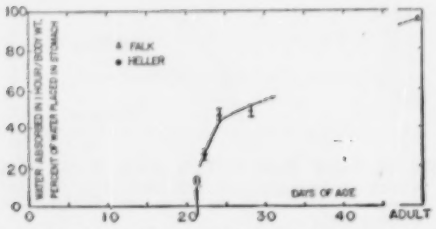

FIG. 48. WATER ABSORBED FROM THE ALIMENTARY TRACT IN RATS GIVEN BY STOMACH WATER EQUAL TO 5% OF THE BODY WEIGHT
(Data of Heller, 1947, and Falk, 1955.)

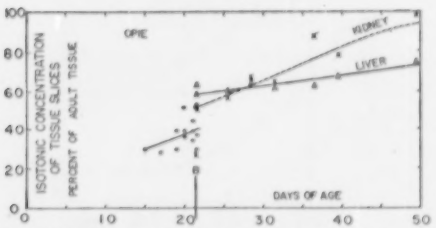

FIG. 49. CONCENTRATION OF NaCl SOLUTION IN WHICH ISOLATED TISSUE SLICES NEITHER SWELL NOR SHRINK DURING 10 MINUTES OF IMMERSION
Each point represents one measurement. (Data of Opie, 1954.)

Water Content as Regulated

We can now consider the regulation of water content in the body as a whole. The relative water content is highest before 15 days of age, being about 93 per cent of the body (Angulo, 1932; Hamilton and Dewar, 1938). Every organ apparently shares in the high water content, at least at birth (Donaldson, 1924). The non-cellular volume is inferred to be very much higher in infants than in adults, at least among other species that have been studied (Flexner et al, 1947; Young, et al., 1943). The amount of this extracellular space is largely governed by the abundance and quality of the cement substances that attach cells to one another; these substances have nothing directly to do with external changes of intake and excretion. There remain for future exploration, therefore, not only the governing factors in cellular composition and volume at each age, but also the controls in extracellular volume at each age.

What can be done to measure tissue interchanges is illustrated by a study of swelling in freshly-isolated tissue slices (Fig. 49). Replicate slices of kidney or of liver are immersed in saline solutions of diverse concentrations in order to estimate in what concentration they neither swell nor shrink. This isotonic concentration of liver increases markedly at about the time of birth. After birth, it progresses more rapidly in kidney than in liver. Factors that govern the apparent isotonic concentrations of tissues are not well understood; plasma osmotic pressure itself changes little with age; but the measurement of isotonicities nevertheless indicates a development, and one that partially governs fluid distribution in vivo.

In mammals the developing embryo is never closed off from a supply of water. Whatever regulations control the volume of muscle cell may also be the ones that operate to control the volume of an ovum. Development follows a course in which we can distinguish stages analogous to those in heat regulation. The transitions from ovum to embryo and fetus (regulation A), thence to free-living individual, unweaned to weaned (regulation C), constitute a continuum. Whether, after birth, a stage also exists in which the infant is more tolerant of water deficit (regulation B) has not been ascertained. Thus we may distinguish stages of regulation, but never an absence of all regulation. The cycle of stages repeats itself in each generation without interruption. But water by itself is not leading the cycle of generations; it is linked with all the other developmental regulations. A kidney, for instance, does not perform without a circulation, and not always with one. Other factors intervene in establishing water exchanges, also in a serial order. A complete description of those factors will involve the whole story of physiological development.

Although regulations are never absent during ontogeny, nevertheless both gradual and sudden shifts occur. These shifts are either transitions from one means of regulation to another, or the acquirement of additional means without loss of the old. When we represent the amount of each process

or regulation upon a common scale, always terming the adult amount 100 per cent, comparisons among very diverse processes and controls become quantitative. Upon the common time scale we are able to observe which transitions are simultaneous. Altogether, we can begin to comprehend the diverse reorganizations through which the infant proceeds. Perhaps they are no greater than those through which it develops before birth, but of those very little is yet known functionally.

Water and solute maintenances are conglomerates of processes and regulations whereby the constancy of bodily composition is maintained. The regulations of composition, like those for heat and for oxygen, may be divided into regulation A, furnished by the parents, and regulation C, developed by the offspring. Extracellular fluid first visibly appears in the blastula as the first cavity forms. Once implantation has occurred, regulation A includes placental interchanges. So long as the maternal plasma has a uniform composition, the fetal plasma may maintain the same or nearly same concentration of each diffusible substance. At birth this source of constancy suddenly disappears. However, regulation A persists in some respects as long as the mother furnishes milk to the offspring. Milk is a metabolic mixture that can be utilized without straining very far the regulatory capacities of the infant; the infant is born with these capacities and not with some upon which milk ingestion will not call.

Regulation B might consist of increased tolerance to concentrations of any of the substances ordinarily appearing in plasma. We have not encountered any special solute-tolerances in infants, but there may be some.

Regulation C represents the infant's intrinsic systems of response. The organs of excretion begin to operate soon after the blood starts to flow in blood vessels, judging by the depositions of dyes in renal tubules (Gersh, 1937). Gradually the ordinary products of excretion appear in amniotic fluid, and some of these products issue from the fetal kidneys. Excretion is practiced before birth, therefore. Perhaps each solute is excreted at a uniform rate, as water is in the first postnatal day. The latitude of regulation enlarges daily, as shown by the concentration of substances in urine (Fig. 35), as well as by the rates of their excretion. Thus the transition is made from the dependent fetus to the semi-dependent infant and finally to the independent weanling. Intakes of water and solutes develop in parallel, being represented prenatally by placental exchanges and postnatally by all the activities involved in drinking and eating. Interchanges among compartments and tissues also change with age, but of them almost none has yet been examined throughout growth.

GENERAL FEATURES OF REGULATIONS

The developments of regulations of three bodily components—heat, oxygen, and water—have now been traced in one species. The results of the three studies are assets from which we may draw larger conclusions. When we compare the three in order to seek similarities and differences, we generalize with the hope of finding rules that apply in the ontogenies of regulations of many components. Some unproven inferences may also be worth noting.

We have observed physiological regulations in the act of developing. The dramatic acquirement of functions exhibits an animal's operations before and after each step, from helplessness to assured performance. The changes with age actually dissect for us the kinds of regulations or controls that ultimately render the individual self-sufficient.

Comparisons within Types of Regulatory Relations

Among the three components whose regulations have been studied here in detail we distinguish (a) common patterns, and (b) simultaneous events. The patterns are easily classified according to the five types found suitable for the general study of regulatory relations.

Regulatory relations of type P related the exchanges of the component to bodily contents of the same component. For heat (Fig. 4) and for water (Fig. 30), partially similar relations were found, in that the exchanges aroused by the shift of content come to act, in the developed rat, in a direction that drives the content toward a norm. For heat, the infant's processes of restoration were easily paralysed by low air temperatures, but the adult's were more powerful. In contrast to the regulations of heat and water, little has been found out about the extent to which oxygen is always kept available in the body. The small size of oxygen content, and the great speed of its uptake and its loss, make difficult the estimation of load in immature individuals.

Regulatory relations of type Q related with one another two concentrations (of solutions), pressures (of oxygen), or temperatures between tissues

and environment, or among tissues. Ease of measurement was chiefly reponsible for the fact that heat regulation was largely revealed by this type of relation (Fig. 1), and oxygen regulation was not so revealed. When oxygen tensimeters shall be as common as thermocouples, more will be known about gradients of oxygen pressures. Oxygen pressures can reach extremes that injure tissues more suddenly than temperatures can. For instance, a sudden interference with the flow of oxygen-rich blood can produce such a state, with its rearrangement of oxygen gradients. For water, the ontogeny of regulation is in the direction of diminishing the exchange with environment per unit of body content. Special organs of alimentation and excretion control most water exchanges, and render vapor tensions and colligative relations of little importance.

Regulatory relations of type R concerned variabilities of bodily contents. The variability of a content has not yet been ascertained at various ages. Bodily contents of heat and of water require longer times to change than do those of oxygen. Reduced contents of oxygen are themselves adequate stimuli to arouse compensations, once the breathing and circulatory responses to hypoxia have developed before birth. The possession of great tolerance to hypoxia by the newborn rat is sometimes believed to imply that asphyxiating environments occur with appreciable frequencies. No studies exist that allow us to compare the natural variations of two or more components in immature mammals. Further, correlations among the diverse functions that vary with supposed randomness, such as breath frequency, tidal volume, oxygen capacity, cardiac output, and other factors, also need to be ascertained at diverse stages of development.

Regulatory relations of type S concerned behaviors that contribute to bodily maintenances. Behaviors of young individuals are prominent as they contribute to heat regulation, for they progress with age from motor incapacity, and possibly sensory indifference, to precise preference among available environments and postures. With respect to water regulation, unwillingness to drink water progresses to expertness in locating and recognizing water. With respect to oxygen regulation, no studies of behaviors appear to have been made. Evidently many motor abilities are linked to specific sensory information about excesses or deficits of heat or water in environment or in body, and the actions that result tend toward bodily maintenance. From the incompetence of the newborn, the actions progress all the way to the competence of the mother to provide not only for herself but for the young as well. For instance, nest building is more frequent and more elaborate when the environment is cooler (Kinder, 1927; Gelineo and Gelineo, 1952).

Finally, relations of type T concerned the means of regulation. An important conclusion is that the effectors overlap, so that they deal with more than one component. Thus, heat regulation employs both oxygen and water in its fulfillment. An oxidase or a breathing reflex subserves all of these regulations, but the controls are sufficiently precise that oxygen supply, heat removal, and water formation are managed with congruity. The congruity extends to all ages; that is one of the requirements of successful ontogeny. Enumeration of the diverse processes and regulators that enter into the management of heat, oxygen, and water would be especially worthwhile if their quantitative participations could be described.

Simultaneous Events

As long as we were studying heat regulation by itself, little opportunity was offered to note that certain events in its regulation were synchronous with other events in, for instance, water regulation. Now, however, we are ready to scan the data at hand for such temporal relationships.

Striking coincidences are found in the response to epinephrine. Two separate effects are absent at 23 days of conceptual age, while five days later they are operative. They are: acceleration of heartbeat (Corey, 1935) and ascorbate depletion of adrenal cortex (Jailer, 1950). So far as known, two separate tissues become sensitive to both epinephrine and nor-epinephrine at about the same age, and the components thus regulated appear to be independent of one another. Empirical recognition of a simultaneity may lead to an effective study of how sensitization to these hormones actually occurs. In addition, it leads us to ask whether the epinephrine effects form a unit-kind of development in the individual (preparation for emergencies, suggested Cannon, 1932), and second, whether comparable complexes of events of other sorts can be identified (i.e., whether constellations are the rule). Neither of these questions receives, so far, any crucial answer from the present study of physiological ontogeny.

Is it possible to compare the contribution that the adrenal cortex makes to cardiac regulation with that it makes to excretory regulation or to some other? This question raises the problem of whether magnitudes can be given to regulations in general. As far as we now know, universal magnitudes are not available. Where exchanges through diverse paths subserve one component, or where energies or molecules are common to two or more components, the effects of specific portions of regulations, such as excretion, can be compared. Otherwise, we are trying to compare dissimilar controls; in an automobile we would be comparing the steering wheel with the accelerator. Dysfunction in either can wreck the vehicle, but that does not make them commensurate. For this reason, we are likely to learn more about regulations by (a) tracing the same portion of the controlling processes through successive ages, and by (b) ascertaining the schedules that various portions bear relative to one another.

Growth of the Internal Environment

Physiologists are impressed with the constancy of the body's internal environment, as represented chiefly by the composition of extracellular fluid and blood plasma. We can partially trace (a) the acquirement of that fluid and (b) the acquirement of its regulation during ontogeny.

Extracellular fluid of the zygote is the uterine fluid furnished by parents. After cleavage has begun, the embryo acquires in the blastula stage a visible body of internal non-cellular fluid. But cement substance interposes between one cell and another even before the blastula stage. The speed of interchange of substances between internal environment and external environment needs to be studied, as do the differences of composition. At first, diffusion may be important in the interchanges; later the existence of circulating blood means that convection predominates. Whereas early exchanges operate between fetus and those fluids filling the fetal-maternal membranes, later exchanges are placental, hence chiefly with the maternal plasma. Whatever inequalities of concentration and whatever clearances may exist between fetal plasma and maternal plasma have scarcely been discovered. When they were known they would tell us whether the fetus contributes any regulation or whether the mother furnishes it all, up to some particular age.

Heat, oxygen, and water regulations do not all await birth before they come into existence. Oxygen is certainly controlled to an extent in the early fetus by, among other factors, the composition of fetal erythrocytes and particularly by the low-pressure dissociation of their oxyhemoglobin. In this sense the fetus "does something" about oxygen at an earlier age than it is known to do anything about water or heat. Water excretion is activated before birth, as shown by the existence of fetal diuresis; whereas in rats, we have no evidence for controlled exchanges of heat until after birth. This demonstrates that not only does each of the three regulations develop its constituent portions serially, but the three also have a certain interrelated succession of their own. Thus, oxygen content of the individual is indispensable to the oxygen consumption that produces heat or that keeps tissues from swelling unduly. The same circulation that carries oxygen also transports water and heat. All three are regulated components of the internal environment at all ages; but if the young animal has to dispense with the regulation of one of them, it seems to survive longest without heat regulation.

Only after birth can most regulation be thought of in terms of the familiar exchanges through special organs. Then oxygen comes in through the lungs, heat goes out through the body surfaces, and water passes out through the kidneys. Exchanges through each organ then come to respond to information fed back from bodily contents. Only after several weeks of progressively more independent life does the young animal correspond to the self-regulated being that Bernard described as relatively free of its environment. For earlier stages than that, our concepts are vague as to how the internal environment persists and as to how the sites of exchange manage to keep its composition near the average. A widespread supposition is that a mammal springs into action at birth endowed with its complement of physiological properties and controls. What we have seen in this study seems to demonstrate that no one control appears suddenly, and that many are operating long before birth, while others arrive long after birth.

At every stage, the exchanges bear some relation to the internal composition and volume. That fact is the simplest statement that can be made about regulation. Diffusion itself corresponds to that relation. But certainly other information passes from the internal environment to the organs of exchange; those organs then respond in specific

ways that achieve the constancy which we observe. How information is selected and mediated is little understood. To the organ physiologist, the chief revelation is that some of the same regulations which characterize the adult are achieved in fetuses, at first without known mediators and organs of exchange, and later with only immature ones.

Further Generalizations

We watched how regulations begin and found that controls have no sudden birth, but that each is "led up to." Just as physical birth is the realization of a stage of development, a step toward independence, so every stage is a flowering long after the bud was organized. We saw heat regulations being built, oxygen regulations emerge, water regulations materialize, all upon overlapping time schedules.

The first generalization to be stated, therefore, is that the initial appearances of functions have a serial order. Functions are in this respect no different from structures, and of course are interdependent with them. The appearance of each represents a sudden or gradual release, as though by the addition of a link or a limiting factor. Striking examples are: the equalizing of heat loss and heat gain in air of 10° at 44 days of age, the response of adrenal glands to cold stimuli at 37 days, the completion of water diuresis at 31 days.

A corollary of the above picture is that partial maturations of function are often in themselves of little consequence to the individual. The first day's growth of hair is as useless as the first blood corpuscle. But provisions are already made for ultimate development of a full and effective complement of each. Moreover, the total insulation provided by the hair is destined to bear a functional relation to the total oxidation of cells, and that to the delivery of oxygen by circulating blood. Again, the fact that the adrenal cortex, when informed by mediators, will respond to cold air that impinges on the rat's skin, is not evident at the age when the adrenals have already learned to produce hormone. The futility of beginnings per se is familiar to those who have carefully considered developmental processes, but needs to be stated as specifically as possible.

Can we compare the ages at which the three regulations (heat, oxygen, and water) matured? Proceeding in the manner of Table 1, we find that while heat regulations are half-grown at 33 to 36 days of age, oxygen regulations (from Figures 20 and 24) are half-grown at 30 days, and water regulations (from Figures 34 to 37) are half-grown at 30 days. We can conclude that heat regulation matures somewhat later than the other two. Whether our estimates of ages are unbiased by our emphasis on postnatal events cannot be determined at present; in other words, the age mentioned may not properly represent the over-all factors of oxygen regulation, for instance. Nevertheless, the method outlined should become more valuable as information is fed to it.

Within any one regulation, also, we found transitions in specific properties. Thus we were able to see the steps by which operating controls were added to, and occasionally superimposed upon, the controls present earlier. No finer dissection of regulations seems yet available, by use of experimental agents, than the dissection that occurs naturally in every immature individual. From the study of dissected regulations we conclude that regulations are established in stages, and maturity consists in completing the number and the interplay of formed controls. To find whether this is so was the principal aim of our investigation.

If we should line up all the graphs in which age is the abscissa, we could again view the relative movement of each function during ontogeny. For instance, prenatally the oxygen consumption diminishes, later the heart-beat starts and its frequency increases, a few days later water excretion begins. One after another, functions wax from nothing to maximum (0 to 100% on the graphs), and near there they stabilize for life. This is the sort of panorama that can be obtained from superimposed age diagrams; but the panorama is not merely descriptive, for it tells us that the serial developments are interlocked. The interlocking itself may be the most fundamental feature of regulations that we can recognize today. Two remarks about age studies can be interjected here.

First we glean a useful lesson in logic from the fact that not all successions of events have any direct connection with one another. *Post hoc non propter hoc.* For, while development with age follows a rather fixed schedule, only in limited instances is an early development of a function prerequisite to a later development. Even when the early development is indispensable, it may be later replaced; thus, oxygen exchange through the placenta is adequate up to a particular stage of development, though later the placenta is suddenly rejected and

the lungs take over that exchange. Is there any criterion other than reasoning and rationalization by which an antecedent prerequisite to oxygen maintenance, such as a movement of blood, can be distinguished from a mere predecessor, such as a thickening of skin? Perhaps only experimental destruction or blocking of the antecedent function can decide the difference; this procedure constitutes another form of physiological dissection.

Second, what sort of control prevents a function from developing farther than it does? Heat production (chemical regulation) might mount severalfold more; water diuresis might be still more prompt. A partial answer lies in the heterogonies among diverse functions that are recognized in animals beyond infancy. Thus, in rats, basal heat production comes to be a fairly constant correlative body weight (Davis, 1937; Kibler and Brody, 1942), of heart-beat frequency (Grad, 1953), of breath frequency (Adolph, 1951), and of a host of other factors, the ones best known being factors of chemical composition (Needham, 1942). This multiplicity of orderly relationships means that regulators are shared in common. Probably it implies that each component influences all others. Such mutual influences are, inextricably, both excitations and inhibitions, since they insure relations that most often are power factors (heterogonic).

Another general pattern consists in the parallel courses of regulations A, B, and C. Parental provisions, youthful tolerances, and intrinsic controls supplement one another in each of the three components studied, and in many more. Figure 15 could be relabelled to represent oxygen regulations or water regulations in place of heat regulations; and the three diagrams could be generalized to represent three coordinated contributions to the maintenance of all developing individuals. The diagrams would call attention to the transitory character of the provisions for maintaining the properties of young individuals; only the adult shows anything approaching a permanently steady state.

Thus each process or control appears from unrecognized precursors, increases rapidly during one range of ages, and then joins the march of the steady disproportionalities. Rapidity of increase allows the function to become sufficient to be effective. The control over the increase might be intrinsic to some localized pacemaker. But the initial control that triggers the early development of the regulation, and the final control that limits and maintains its capacity, are evidently in part outside the phenomenon regulated, whether it concerns heat, oxygen, or water.

Immaturity can be viewed speculatively as a stage of development during which regulations that can operate more economically are gradually established. Often the fetus or infant clumsily meets circumstances that the adult meets easily and quickly. By moderate investments of extra capital, the infant not only survives but also prepares itself for continued cheaper maintenance. An evidence of this is the fact that minimal metabolism per unit of mass characterizes the adult. One can even say that entropy-production is minimal in the adult, its adjustments being so steady. Conversely, maturing is a costly process for two reasons: one, capital expenditures are being made to add abilities for future use, and two, maintenance expenditures are meanwhile greater in the absence of those abilities. Such speculations are impossible to test in any conclusive way at the present time, but they serve to suggest another concept of what the physiologically-growing animal is doing.

We tend to speak as though the regulations with which the adult is endowed are the only adequate ones, superior to those of infants. In doing so, we recognize that they are in use longer than those of infants. Actually we are not justified in believing that adult regulations could successfully be imposed upon infants. As far as we know, each stage of development is functionally complete in its own right, and the common supposition that the adult stage enjoys special advantages cannot rigorously be sustained, because we have no criterion of advantages and disadvantages other than the frequency of survival in natural circumstances.

Some General Experimental Methods

Most of the studies on which our account of physiological ontogeny is based consisted in particular arrangements of selected observations upon rats or other animals at certain ages. They were chiefly descriptive. They may form a background for further penetrating experiments, and therefore we may state what kinds of experiments are likely to reveal how regulatory activities are born.

Approximately, two general methods are available. We may add agents or tissues to the developing animal, or we may delete from or block the animal's functions. The two categories need not be

kept separate, since both are designed to influence development.

Additions may be tried at diverse ages, whereupon they or their effects will prove compatible or incompatible with the individual's survival after the particular age. Implantation of tissues, transfusions of blood, and parabiosis are familiar techniques in adult mammals; they have been only partially tested in fetus and newborn.

Deletions may be either mechanical or chemical. By them one ascertains whether development will be steered from its usual course, and what specific regulations fail or shift. Organectomies, nerve sectionings, and local ischemias modify in a great variety of mechanical ways. Incomplete diets and chemical blocking agents modify both generally and specifically. Radiations (Wilson et al., 1953; Evans et al., 1942) and general hypothermia and hyperthermia (Hsu, 1948) are effective tools. Controlled genetic influences may be utilized, as in congenital atrophy of kidneys (Morgan, 1953).

What may be expected from experimental interferences with the development of regulations? We may learn whether the modifications are compatible with survival, whether the serial order of development is fixed or movable, which antecedents are indispensable, and what compensations the organism musters. No doubt the whole science of "abnormal" development will contribute to the above questions. In turn, the viewpoint of regulations furnishes means of assessing the functional alterations found. For instance, we learn not merely that a rat thrives until birth without kidneys (Morgan, 1953), but also how much water diuresis can later be shown in the presence of one-half the usual kidney mass (Falk, 1955). We learn also that no direct measure of kidney mass will alone foretell what water-excretory functions will become available during the first ten postnatal days.

Diverse Regulations

The three components (heat, oxygen, water) whose regulations we have here studied in detail may or may not be representative of components in general. These three regulations are found to develop postnatally in considerable part. When we study the many other components that are regulated intrinsically in every cell, less emphasis might then appropriately be placed on late stages of development. No doubt we know more about heat and water in ontogeny by virtue of their postnatal scheduling; postnatally, they are open to direct observation.

If we try to list components whose regulations can be traced early in embryonic life, they are found to be many. Growth itself has innumerable functional controls. Contractility, conduction, specific localization, specific secretion, synthesis, differentiation of proteins, and enzymic activities all represent regulations of the types we should investigate. No one of these components, probably, is unregulated at any moment, from fertilization until adult somatic death.

Each regulation studied (such as heat control) appears to require for its operation a particular set of processes. The set overlaps only in part that which is required for some other regulation (such as water control). Each set results from serial differentiations. If we suppose that an animal regulates a hundred or a thousand of its functions, and each property requires a control over gain and a control over loss, we see that a huge number of controls finally accumulates. During every day of development, dozens of them come into operation. I see no way of counting fewer than that. When we further consider that each new control fits into those already established, and into those still to come, the picture we form is a complex one indeed. The organism is nothing less than the picture portrays, and it is a stupendous task merely to describe and understand superficially the individual items concerned in these controls. Nothing less than that task will supply a reasonably complete account of the development of physiological regulations.

We watched the fetus unwind into an organism that controlled its maintenances. We noted that at any one age, all individuals of the species had like maintenances. These maintenances are the livelihood of the organism; physiologically considered, they are the organism. At fertilization, the individual is not at all similar functionally to the newborn or the adult. Yet, we recognize that the zygote is destined to be a newborn. We are privileged to see it become so. Without understanding how the metamorphosis comes about, we recognize the inevitable and persistent course of development of an organism that works. At a hundred turns, the maintenances could go wrong; actually the paths which development follows ultimately provide functions fit for life. The morphological description of development has already pictured this orderliness. Intricate and amazing as that description has become, it falls far short, in my estimation, of the picture of splendid orderliness revealed in the

serial establishment of controls over each and all of the physiological properties, in the self-guided and sure course that leads to the steady states of adulthood.

ACKNOWLEDGMENTS

Part of the work represented here was supported by a grant of the National Science Foundation. Aid in preparation of data was given by P. A. Hoy.

LIST OF LITERATURE

ADDIS, T., and GRAY, H. 1950. Body size and organ weight. *Growth*, 14: 49–80.

ADOLPH, E. F. 1935. Oxygen tension and urine production in frogs. *Amer. J. Physiol.*, 111: 75–82.

——. 1943. *Physiological Regulations*. Cattell, Lancaster. 502 pp.

——. 1947. Tolerance to heat and dehydration in several species of mammals. *Amer. J. Physiol.*, 151: 564–575.

——. 1948. Tolerances to cold and anoxia in infant rats. *Amer. J. Physiol.*, 155: 366–377.

——. 1949. Quantitative relations in the physiological constitutions of mammals. *Science*, 109: 579–585.

——. 1951. Responses to hypothermia in several species of infant mammals. *Amer. J. Physiol.*, 166: 75–91.

——, BARKER, J. P., and HOY, P. A. 1954. Multiple factors in thirst. *Amer. J. Physiol.*, 178: 538–562.

ALTLAND, P. D., and ALLEN, E. 1952. Studies of degenerating sex cells in immature mammals, III. *J. Morph.*, 91: 541–553.

AMES, R. G. 1953. Urinary water excretion and neurohypophysical function in full term and premature infants shortly after birth. *Pediatrics*, 12: 272–282.

ANGULO y GONZALEZ, A. W. 1932. The prenatal growth of the albino rat. *Anat. Rec.*, 52: 117–138.

ANTOSCHKINA, E. D. 1939. Ueber die Ausbildung der Wärmeregulierung im Laufe der Ontogenese, I und II. *Fiz. Zh.*, 26: 1–15, 16–29.

ARATAKI, M. 1926. The postnatal growth of the kidney, with special reference to the number and size of the glomeruli (Albino Rat). *Amer. J. Anat.*, 36: 399–436.

ASHBY, W., and SCHUSTER, E. M. 1950. Carbonic anhydrase in the brain of the newborn in relation to functional maturity. *J. biol. Chem.*, 184: 109–116.

——, GARZOLI, R. F., and SCHUSTER, E. M. 1952. Relative distribution patterns of three brain enzymes, carbonic anhydrase, choline esterase and acetyl phosphatase. *Amer. J. Physiol.*, 170: 116–120.

AUSTIN, C. R., and BRADEN, A. W. H. 1954. Time relations and their significance in the ovulation and penetration of eggs in rats and rabbits. *Aust. J. biol. Sci.*, 7: 179–194.

BARCROFT, J. 1947. *Researches on Prenatal Life*. Thomas, Springfield. 292 pp.

——, and KARVONEN, M. J. 1948. The action of carbon dioxide and cyanide on foetal respiratory movements; the development of chemoreflex function in sheep. *J. Physiol.*, 107: 153–161.

BARKER, J. N. 1956. Thesis, Duke University.

BAUER, D. J. 1939. Vagal reflexes appearing in asphyxia in rabbits at different ages. *J. Physiol.*, 95: 187–202.

BERNARD, C. 1878. *Leçons sur les phénomènes de la vie communs aux animaux et aux vegetaux*. Baillière, Paris. 2 Tomes.

BERTALANFFY, L., and PIROZYNSKI, W. J. 1951. Tissue respiration and body size. *Science*, 113: 599–600.

BEZNAK, M. 1954. The behavior of the weight of the heart and the blood pressure of albino rats under different conditions. *J. Physiol.*, 124: 44–63.

BIESELE, J. J. 1946. The size of somatic chromosomes at different ages in the rat. *J. Geront.*, 1: 433–440.

BLACK, A., and SWIFT, R. W. 1943. The critical temperature for the albino rat as affected by feeding. *J. Nutr.*, 25: 127–136.

BLANDAU, R. J., and SODERWALL, A. L. 1941. Postparturitional heat and the time of ovulation in the albino rat. Data on parturition. *Anat. Rec.*, 81: 419–431.

BOELL, E. J., and NICHOLAS, J. S. 1948. Respiratory metabolism of the mammalian egg. *J. exp. Zool.*, 109: 267–281.

BOYLE, R. 1670. New pneumatical experiments about respiration. *Philos. Trans.*, 5: 2011–2031.

BRADEN, A. W. H., and AUSTIN, C. R. 1954. The fertile life of mouse and rat eggs. *Science*, 120: 610–611.

BRITTON, S. W., and KLINE, R. F. 1945. Age, sex, carbohydrate, adrenal cortex and other factors in anoxia. *Amer. J. Physiol.*, 145: 190–202.

BRODY, E. B. 1943. Development of homeothermy in suckling rats. *Amer. J. Physiol.*, 139: 230–232.

BRUNER, H. D., VAN DE ERVE, J., and CARLSON, A. J. 1938. The blood picture of rats from birth to 24 days of age. *Amer. J. Physiol.*, 124: 620–626.

BUCHANAN, A. R., and HILL, R. M. 1947. Temperature regulation in albino rats correlated with determinations of myelin density in the hypothalamus. *Proc. Soc. exp. Biol., N. Y.*, 66: 602–608.

BURLINGAME, P., LONG, J. A., and OGDEN, E. 1942. Blood pressure of the fetal rat and its response to renin and angiotonin. *Amer. J. Physiol.*, 173: 473–484.

BURN, J. H., TRUELOVE, L. H., and BURN, I. 1945. The antidiuretic action of nicotine and of smoking. *Brit. med. J.*, I: 403–406.

BUTCHER, E. O. 1934. The hair cycles in the albino rat. *Anat. Rec.*, 61: 5–19.

——. 1943. The oxygen consumption of the skin during the hair cycle in the white rat *Amer. J. Physiol.*, 138: 408–411.

——. 1954. Fluid loss through epidermis of the rat and factors affecting it. *Proc. Soc. exp. Biol., N. Y.*, 87: 511–513.

——, and GROKOEST, A. W. 1941. The influence of tissue fluid on hair growth. *Growth*, 5: 175–181.

CANNON, W. B. 1932. *The Wisdom of the Body.* Norton, New York. 312 pp.

CAPEK, K., HAHN, P., KRECEK, J., and MARTINEK, J. 1956. Studie o fysiologii novorozenych mladat. *Rozpr. české Akad.*, 66: xii, 1–97.

CARLYLE, A. 1948. An integration of the total oxygen consumption of the sheep foetus from that of the tissues. *J. Physiol.*, 107: 355–364.

CHESLER, A., and HIMWICH, H. E. 1944. A comparative study of the rates of oxidation and glycolysis in the cerebral cortex and brain stem of the rat. *Amer. J. Physiol.*, 141: 513–517.

CHEYMOL, J., and LEVASSORT, C. 1952. Regulation thermique et résistance a l'hypoxémie. *Bull. Soc. Chim. biol., Paris* 34: 813–818.

COHNSTEIN, J., and ZUNTZ, N. 1884. Untersuchungen über das Blut, den Kreislauf und die Athmung beim Säugethier—Fötus. *Arch. ges. Physiol.*, 34: 173–233.

COLD SPRING HARBOR SYMPOSIUM, Vol. 19. 1954. *The Mammalian Fetus: Physiological Aspects of Development.* 225 pp.

CONTOPOULOS, A. N., VAN DYKE, D. C., SIMPSON, M. E., LAWRENCE, J. H., and EVANS, H. M. 1954. Failure of newborn rats to respond to hypoxia with increased erythropoiesis. *Proc. Soc. exp. Biol., N. Y.*, 86: 713–715.

COREY, E. L. 1935. Observations on cardiac activity in the fetal rat. *J. exp. Zool.*, 72: 127–145.

COVELL, W. P. 1926. Quantitative cytological studies on the renal tubules. 1. Nucleocytoplasmic ratio. *Anat. Rec.*, 34: 61–73.

CRAIGIE, E. H. 1924. Changes in vascularity in the brain stem and cerebellum of the albino rat between birth and maturity. *J. comp. Neurol.*, 38: 27–48.

CRESKOFF, A. J., FITZ-HUGH, JR., T., and FARRIS, E. J. 1949. Hematology of the rat. Methods and standards. Ch. 14 in *The Rat in Laboratory Investigation* (Farris, E. J., and J. Q Griffith, Jr.) Lippincott, Philadelphia. 542 pp.

CROSS, K. W., HOOPER, J. M. D., and LORD, J. M. 1954. Anoxic depression of the medulla in the new-born infant. *J. Physiol.*, 125: 628–640.

CZECHOSLOVAK ACADEMY OF SCIENCE. 1956. Conference on Problems of Physiology in the Preweaning Period in Man and Mammals (Abstracts).

DALY, H., WELLS, L. J., and EVANS, G. 1947. Experimental evidence of the secretion of urine by the fetal kidney. *Proc. Soc. exp. Biol., N. Y.*, 64: 78–80.

DAVIS, J. E. 1937. The effect of advancing age on the oxygen consumption of rats. *Amer. J. Physiol.*, 119: 28–33.

DICKER, S. E., and TYLER, C. 1953. Vasopressor and oxytocic activities of the pituitary glands of rats, guinea-pigs and cats and of human foetuses. *J. Physiol.*, 121: 206–214.

DONALDSON, H. H. 1924. *The Rat.* 2nd ed. Wistar, Philadelphia. 469 pp.

DONALDSON, J. C. 1919. The relative volumes of the cortex and medulla of the adrenal gland in the albino rat. *Amer. J. Anat.*, 25: 291–298.

DUMM, M. E. 1943. Histochemical studies of the liver of the rat during embryonic development. *J. cell. comp. Physiol.*, 21: 27–39.

EDWARDS, W. F. 1824. *De l'influence des agens physiques sur la vie.* Crochard, Paris. 654 pp.

EVANS, T. C., GOODRICH, J. P., and SLAUGHTER, J. C. 1942. Temperature and radiosensitivity of skin of new-born rats. IV. Effects of decreased circulation and breathing during irradiation. *Radiology* 38: 201–206.

FAIRFIELD, J. 1948. Effects of cold on infant rats: body temperature, oxygen consumption, electrocardiograms. *Amer. J. Physiol.*, 155: 355–365.

FALK, G. 1955. Maturation of renal function in infant rats. *Amer. J. Physiol.*, 181: 157–170.

FAZEKAS, J. F., ALEXANDER, F. A. D., and HIMWICH, H. E. 1941. Tolerance of the newborn to anoxia. *Amer. J. Physiol.*, 134: 281–287.

FLEXNER, L. B., and POHL, H. A. 1941. The transfer of radioactive sodium across the placenta of the white rat. *J. cell. comp. Physiol.*, 18: 49–59.

——, WILDE, W. S., PROCTOR, N. K., VOSBURGH, G. J., HELLMAN, L. M. and COWIE, D. B. 1947. The estimation of extracellular and total body water in the newborn human infant with radioactive sodium and deuterium oxide. *J. Pediat.*, 30: 413–415.

FORBES, G. B. 1955. Inorganic chemical heterogony in man and animals. *Growth*, 19: 75–87.

FRANKLIN, K. J., MCGEE, L. E., and ULLMANN, E. A. 1951. Effects of severe asphyxia on the kidney and urine flow. *J. Physiol.*, 112: 43–53.

FRASER, D. A. 1928. The development of the skin of the back of the albino rat until the eruption of the first hairs. *Anat. Rec.*, 38: 203–224.

FRYERS, G. R., and BERLIN, N. I. 1952. Mean red cell life of rats exposed to reduced barometric pressure. *Amer. J. Physiol.*, 171: 465–470.

GELINEO, S. 1934. Influence du milieu thermique d'adaptation sur la thermogénèse des homéothermes. *Ann. Physiol.*, 10: 1083–1115.

——, and GELINEO, A. 1952. La temperature du nid du rat et sa signification biologique. *Bull. Acad. serbe Sci. math. nat. (Sci. nat.)*, 197–210.

GERSH, I. 1937. The correlation of structure and function in the developing mesonephros and metanephros. *Contr. Embryol. Carneg. Instn*, 26: 33–58.

GIAJA, J. 1925. Le métabolisme de sommet et le quotient métabolique. *Ann. Physiol.*, 1: 596–627.

GOSS, C. M. 1938. The first contractions of the heart in rat embryos. *Anat. Rec.*, 70: 505–524.

——. 1942. The physiology of the embryonic mammalian heart before circulation. *Amer. J. Physiol.*, 137: 146–152.

GRAD, B. 1953. Changes in oxygen consumption and heart rate of rats during growth and ageing: role of the thyroid gland. *Amer. J. Physiol.*, 174: 481–486.

GULICK, A. 1937. The development of temperature control in infant rats. *Amer. J. Physiol.*, 119: 322.

HAMILTON, B., and DEWAR, M. M. 1938. The relation between water and dry substance in the body of the rat, before and after birth. *Growth*, 2: 13–23.

HARDWICK, D. C. 1954. Age changes in the histamine content of rat skin. *J. Physiol.*, 124: 157–165.

HART, J. S. 1950. Interrelations of daily metabolic cycle, activity and environmental temperature of mice. *Canad. J. Res.*, D, 28: 293–307.

——. 1951. Calorimetric determination of average body temperature of small mammals and its variation with environmental conditions. *Canad. J. Zool.*, 29: 224–233.

HARVEY, W. 1651. *Exercitationes de generatione animalium*. Pulleyn, London. 301 pp.

HATAI, S. 1918. The refractive index of the blood serum of the albino rat at different ages. *J. biol. Chem.*, 35: 527–552.

HELLER, H. 1947. The response of newborn rats to administration of water by the stomach. *J. Physiol.*, 106: 245–255.

——. 1952. The action and fate of vasopressin in newborn and infant rats. *J. Endocrin.*, 8: 214–223.

HEYMANN, W., and SALEHAR, M. 1949. Blood pressure in the rat. *Proc. Soc. exp. Biol., N. Y.*, 72: 191–192.

HICKS, S. P. 1953. Developmental brain metabolism. *Arch. Path. (Lab. Med.)*, 55: 302–327.

HIMWICH, H. E., BERNSTEIN, A. O., HERRLICH, H., CHESLER, A., and FAZEKAS, J. F. 1942. Mechanisms for the maintenance of life in the newborn during anoxia. *Amer. J. Physiol.*, 135: 387–391.

——, FAZEKAS, J. F., and HOMBURGER, E. 1943. Effect of hypoglycemia and anoxia on the survival period of infant and adult rats and cats. *Endocrinology*, 33: 96–100.

HÖKFELT, B. 1951. Noradrenaline and adrenaline in mammalian tissues. *Acta physiol. Scand.*, 25, Suppl. 92. 134 pp.

HOLTKAMP, D. E., HILL, R. M., LONGWELL, B. B., RUTLEDGE, E. K., and BUCHANAN, A. R. 1949. Failure of adrenal cortical hormone to protect against cold in young normal and adrenalectomized rats. *Amer. J. Physiol.*, 156: 368–376.

HOY, P. A., and ADOLPH, E. F. 1956. Diuresis in response to hypoxia and epinephrine in infant rats. *Amer. J. Physiol.*, 187: 32–40.

HSU, C. Y. 1948. Influence of temperature on development of rat embryos. *Anat. Rec.*, 100: 79–90.

IOB, V., and SWANSON, W. W. 1938. Mineral growth. *Growth*, 2: 253–256.

IRWIN, E., BUCHANAN, A. R., LONGWELL, B. B., HOLTKAMP, D. E., and HILL, R. M. 1950. Ascorbic acid content of adrenal glands of young albino rats after cold and other stresses. *Endocrinology*, 46: 526–535.

ITANO, H. A. 1953. Human hemoglobin. *Science*, 117: 89–94; 118: 116–117.

JACOBSON, F. H. 1954. Calorimetry of rats immersed in cool water. *Amer. J. Physiol.*, 176: 287–296.

JAILER, J. W. 1950. The maturation of the pituitary-adrenal axis in the newborn rat. *Endocrinology*, 46: 420–425.

JONES, P. E. H. 1951. The absorption of glucose and xylose by adult and newborn rats. *J. Physiol.*, 113: 276–282.

JOSIMOVICH, J. B., LADMAN, A. J., and DEANE, H. W. 1954. A histophysiological study of the developing adrenal cortex of the rat during fetal and early postnatal stages. *Endocrinology*, 54: 627–639.

KENSLER, C. J., RUDDEN, M., SHAPIRO, E., and LANGEMANN, H. 1952. Choline oxidase activity in young rats. *Proc. Soc. exp. Biol., N. Y.*, 79: 39–42.

KIBLER, H. H., and BRODY, S. 1942. Metabolism and growth rate of rats. *J. Nutr.*, 24: 461–468.

KIIL, V. 1949. Experiments on the hair slope and hair pattern in rats. *J. exp. Zool.*, 110: 397–439.

KINDER, E. F. 1927. A study of the nest-building activity of the albino rat. *J. exp. Zool.*, 47: 117–161.

KLEIBER, M., COLE, H. H., and SMITH, A. H. 1943. Metabolic rate of rat fetuses in vitro. *J. cell. comp. Physiol.*, 22: 167–176.

KUNKEL, H. O., and CAMPBELL JR., E. J. 1952. Tissue cytochrome oxidase activity and body weight. *J. biol. Chem.*, 198: 229–236.

LANDAUER, W. 1942. Form and function in frizzle fowl; the interaction of hereditary potentialities and environmental temperature. *Biol. Symp.*, 6: 127–166.

LEE, M. O. 1929. Determination of the surface area of the white rat with its application to the expression of metabolic results. *Amer. J. Physiol.*, 89: 24–33.

LE GALLOIS, J. J. C. 1812. *Expériences sur le principe de la vie.* D'Hautel, Paris. 364 pp.

LE GALLOIS, C. J. J. 1834. *Fragments d'un mémoire sur le temps les jeunes animaux peuvent être, sans danger, privés de la respiration, soit à l'époque de l'accouchement, lorsqu'ils n'ont point encore respiré, soit à differents ages après leur naissance.* Didot, Paris. 160 pp.

LONG, C. N. H. 1947. The relation of cholesterol and ascorbic acid to secretion of the adrenal gland. *Recent Progr. Hormone Res.*, 1: 99–122.

LOWREY, L. G. 1913. The growth of the dry substance in the albino rat. *Anat. Rec.*, 7: 143–168.

MANDEL, P., and BIETH, R. 1951. La repartition des diverses fractions lipidiques au cours du développement du cerveau chez le rat. *Bull. Soc. Chim. biol., Paris*, 33: 973–981.

MCCASHLAND, B. W. 1951. A study of metabolism changes in young rats. *Growth*, 15: 1–9.

METZLER, C. J., and HUMM, D. G. 1951. The determination of cholinesterase activity in whole brains of developing rats. *Science*, 113: 382–383.

MILLER, L. L., and BALE, W. F. 1954. Synthesis of all plasma protein fractions except gamma globulins by the liver. *J. exp. Med.*, 99: 125–132.

MOON, H. D. 1940. Effect of adrenocorticotropic hormone in 4 day old rats. *Proc. Soc. exp. Biol., N. Y.*, 43: 42–44.

MORGAN, W. C. 1953. Inherited congenital kidney absence in an inbred strain of rats. *Anat. Rec.*, 115: 635–639.

NEEDHAM, J. 1942. *Biochemistry and Morphogenesis.* The Univ. Press, Cambridge. 785 pp.

NEGELEIN, E. 1925. Ueber die glykolytische Wirkung des embryonalen Gewebes. *Biochem. Z.*, 165: 122–133.

NICHOLAS, J. S. 1928. The determination of the amount of hemoglobin present in rat fetuses during development. *Amer. J. Physiol.*, 183: 499–501.

——. 1947. Experimental approaches to problems of early development in the rat. *Quart. Rev. Biol.*, 22: 179–195.

——. 1949. Experimental methods and rat embryos. Ch. 4 in *The Rat in Laboratory Investigation* (Farris, E. J., and J. Q. Griffith Jr.). Lippincott, Philadelphia. 542 pp.

——. 1950. Development of contractility. *Proc. Amer. phil. Soc.*, 94: 175–183.

OPIE, E. L. 1954. Osmotic activity of tissue during fetal and postnatal growth. *J. exp. Med.*, 100: 405–416.

PEMBREY, M. S. 1895. The effect of variations in external temperature upon output of carbonic acid and the temperature of young animals. *J. Physiol.*, 18: 363–379.

POTTER, V. R., SCHNEIDER, W. C., and LIEBL, G. J. 1945. Enzyme changes during growth and differentiation in the tissues of the newborn rat. *Cancer Res.*, 5: 21–24.

PREYER, W. 1885. *Specielle Physiologie des Embryo.* Grieben, Leipzig. 643 S.

RINFRET, A. P., and HANE, S. 1955. The adrenal ascorbic acid-depleting capacity of extracts of the infant rat pituitary gland. *Endocrinology*, 56: 341–344.

ROBINSON, J. R. 1949. Some effects of glucose and calcium upon the metabolism of kidney slices from adult and newborn rats. *Biochem. J.*, 45: 68–74.

SCHÜLER, W. 1943. Beziehungen zwischen Organstoffwechsel und Lebensalter von Ratten. *Helv. physiol. acta*, 1: 105–112.

SELLE, W. A., and WITTEN, T. A. 1941. Survival of the respiratory (gasping) mechanism in young animals subjected to anoxia. *Proc. Soc. exp. Biol., N. Y.*, 47: 495–497.

SHAPIRO, B., and WERTHEIMER, E. 1943. Phosphorolysis and synthesis of glycogen in animal tissues. *Biochem. J.*, 37: 397–403.

SILVETTE, H. 1943. Some effects of low barometric pressures on kidney function in the white rat. *Amer. J. Physiol.*, 140: 374–386.

SINCLAIR, R. G. 1930. The metabolism of the phospholipids. II. The influence of growth on the phospholipid (and cholesterol) content of the white rat. *J. biol. Chem.*, 88: 575–587.

SIPPEL, T. O. 1954. The growth of succinoxidase activity in the hearts of rat and chick embryos. *J. exp. Zool.*, 126: 205–221.

SMITH, CHRISTIANNA. 1932. The post-embryonic development of the erythrocyte of the albino rat. *J. Path. Bact.*, 35: 717–726.

SMITH, CLEMENT A. 1953. *The Physiology of the Newborn Infant.* 2nd ed. Thomas, Springfield. 348 pp.

SPERRY, W. M. 1955. Lipides of the brain during early development in the rat. In *Biochemistry of the Developing Nervous System* (H. Waelsch, ed.), 261–267. Academic Press, New York. 537 pp.

STICKNEY, J. C., NORTHUP, D. W., and VAN LIERE, E. J. 1946. The effect of anoxic anoxia on urine secretion in anesthetized dogs. *Amer. J. Physiol.*, 147: 616–621.

STOERK, H. C., and ZUCKER, T. F. 1946. Relative growth of the kidney in male rats. *Proc. Soc. exp. Biol., N. Y.*, 61: 297–299.

THIGPEN, L. W. 1940. Histology of the skin of a normally hairless rodent. *J. Mammal.*, 21: 449–456

TOBIN, C. E. 1939. The influence of adrenal destruction on the prenatal development of the albino rat. *Amer. J. Anat.*, 65: 151–177

OTH, L. A. 1937. Urine formation under anoxia in dogs. *Amer. J. Physiol.*, 119: 127–139.

—. 1940. Urine excretion during anoxia from normal and denervated kidneys in dogs with and without adrenal glands. *Amer. J. Physiol.*, 129: 532–538.

OYAMA, I. 1919. Relative abundance of serum proteins in albino rats at different ages. *J. biol. Chem.*, 38: 161–166.

ISCHIRGI, R. D. 1946. Carotid receptors essential in the gasping of the isolated rat head. *Proc. Soc. exp. Biol., N. Y.*, 63: 397–398.

——, and GERARD, R. W. 1947. The carotid-mandibular reflex in acute respiratory failure. *Amer. J. Physiol.*, 150: 358–364.

TYLER, D. B. 1942. Effect of malonate and iodoacetate on respiration of brains of rats of various ages. *Proc. Soc. exp. Biol., N. Y.*, 49: 537–539.

WALKER, J. 1954. Fetal and adult hemoglobin in the blood of the human fetus. *Cold. Spr. Harb. Sym. quant. Biol.*, 19: 141–142.

WELLS, L. J. 1946. Experimental acceleration of secretion of urine in fetal rats. *Proc. Soc. exp. Biol., N. Y.*, 62: 287–289.

WILSON, J. G., BRENT, R. L., and JORDAN, H. C. 1953. Differentiation as a determinant of the reaction of rat embryos to X-irradiation. *Proc. Soc. exp. Biol., N. Y.*, 82: 67–70.

WINDLE, W. F. 1940. *Physiology of the Fetus.* Saunders, Philadelphia. 249 pp.

WINTROBE, M. M., and SHUMACKER JR., H. B. 1936. Erythrocyte studies in the mammalian fetus and newborn. *Amer. J. Anat.*, 58: 313–328.

WOLFF, B. 1904. Ueber experimentelle Erzeugung von Hydramnion. *Arch. Gynaek.*, 71: 224–257.

——. 1909. Weitere experimentelle Beiträge zur Physiologie des Fruchtwassers. *Arch. Gynaek.*, 89: 177–229.

YOUNG, W. F., MCCANCE, R. A., JONES, A., and DOBBS, R. 1943. Discussion on water metabolism in sick and healthy infants. *Proc. R. Soc. Med.*, 36: 219–221.

HAECKEL, DARWIN, AND ECOLOGY

By ROBERT C. STAUFFER

University of Wisconsin

INTRODUCTION

THE TERM ecology was invented by a theoretical morphologist who was not a distinguished student of ecology and who was outspokenly hostile to one of the most significant programs of ecological research of his day, the controversial but influential pioneering venture to establish plankton studies on a quantitative basis. This paradox of the position of Ernst Haeckel (1834–1919) in the history of ecology poses the problem for this paper. Haeckel's major contributions may be best understood as an immediate byproduct of his aim to interpret Darwin's thought for the scientific world of Germany rather than as the logical outgrowth of his own research. In his work as a field naturalist, Haeckel showed a painter's eye for the beauties of nature, and he was an ardent collector whose travels ranged from Norway, Helgoland, the Canaries, and Messina to the Red Sea, Cylon, and Java. This wide and vivid experience brought him some appreciation of ecological points of view, but Haeckel did not display any notable insight into the dynamic principles of ecology. My purpose here is to examine the nature and the personal limitations of Haeckel's contributions to the science he named and to demonstrate its Darwinian derivation.

HAECKEL AND DARWINISM

Ecology was introduced into the vocabulary of science in 1866 in Haeckel's *Generelle Morphologie*. This was the first of a number of books which Haeckel wrote to forward the cause of Darwinism as he saw it, and we must start with a glance at the general background of Haeckel's early enthusiasm for Charles Darwin (1809–1882).

Even as a medical student at Würzburg in 1853, in writing home to propose books for family vacation reading, Haeckel had been appreciative of the "excellent travels of Darwin" (Haeckel, 1852–1856, p. 124). In the autumn of 1859, however, when Darwin's *Origin* was published, Haeckel was far from the world of scientific news. He was at Messina on the straits between Sicily and Italy, where he was following the example of his beloved teacher, Johannes Müller (1801–1858), in studying the riches of the sea to be captured with the collecting net. Using the methods which he had learned from Müller at Helgoland in 1854 (Haeckel, 1852–1856, p. 251), Haeckel obtained many new species of Radiolaria to delight his artist's eye. The results of these months of collecting and study at Messina he brought north to form the foundation for his masterpiece—his first huge monograph, *Die Radiolarien*, which was to secure him his appointment as ausserordentlicher Professor in the medical faculty at Jena at the age of 28. It was thus only later, while he was working up his Italian collections, that Haeckel became familiar with the *Origin of Species*.

This encounter was to be a major influence on Haeckel's personal beliefs and on his scientific career. "After my return from Italy in 1860 when I became acquainted with Darwin's work, when I saw in it the way prepared for a mechanistic or monistic solution of the most difficult philosophical problems, then there began to develop within me a unified view of life in the face of which only a few of my long-accustomed and beloved articles of faith could endure any longer" (Haeckel, 1874, p. 333). In his *Radiolarien*, Haeckel used Darwinian concepts in his discussion of the relations of the families of this order, in his consideration of a genealogical table, and his speculations regarding the original primitive type form of the order; and he emphasized the evolutionary significance of transitional forms. Here Haeckel expressed his enthusiasm for the stimulating ideas of the *Origin of Species* and explicitly declared his belief that Darwin's theories "had begun a new epoch for the

systematic scientific study of organic nature" (1862, pp. 231–32). As "incontestably important principles of the greatest significance," Haeckel mentioned not only natural selection and the struggle for existence, but also the mutual relations of organisms (pp. 231–33). The year after making this initial declaration, when Haeckel went up to Stettin for the 1863 Versammlung deutscher Naturforscher und Aerzte, he threw himself into the campaign for Darwin by devoting his speech at the first general session to Darwin's theory of evolution (Haeckel, 1863, 1883).

The very title of Haeckel's next book, *Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie* (Berlin, 1866), shows that this two-volume work was another episode in the Darwinian campaign. The general aim and character of the work can be judged from Haeckel's own comments: (1873, p. [xiii]) "a somewhat comprehensive work, which constituted the first attempt to apply the general doctrine of development to the whole range or organic morphology (Anatomy and Biogenesis), and thus to make use of the vast march onwards which the genius of Charles Darwin has effected in all biological science by his reform of the Descent Theory and its establishment through the doctrine of selection. At the same time, in the 'Generelle Morphologie' the first attempt was made to introduce the Descent Theory into the systematic classification of animals and plants, and to found a 'natural system' on the basis of genealogy; that is, to construct hypothetical pedigrees for the various species of organisms." Thus Haeckel intended to present not only a broad synthesis of morphology but also a survey of biology from a Darwinian point of view, and the logical justification for the introduction of ecology comes simply as the demarcation and naming of one of many notable aspects of Darwin's thought.

THE DARWINIAN CONCEPT OF ECOLOGY

The elements of Haeckel's concept of ecology are to be found in Darwin's *Origin of Species* (1859). It is true that other sources possibly relevant but certainly more remote may be recognized. Some of these Professor van der Klaauw (1936) has discussed in his extensive and informative study of the history of the definitions of ecology. But the importance of Darwin is stressed by Haeckel himself; the influence of other earlier writers seems less immediate if not problematical.

If we search the *Origin* for ecological ideas, the most rewarding chapters are those on the struggle for existence and on natural selection, and here the most general and fundamental ecological concept is that which Darwin usually designated either as the "economy of nature" or as the "polity of nature." Now, among the Linnaean dissertations published in the *Amoenitates Academicae* are both an *Oeconomia naturae* and a *Politia naturae*, and Darwin could very easily have derived his concept directly from the Linnaean school simply by substituting the principle of natural selection for Linnaeus' pious belief in Providence as the direct source of the equilibrium of species and the adaptations discoverable in the order of nature. Darwin gave the cats-to-clover chain as "one more instance showing how plants and animals, most remote in the scale of nature, are bound together by a web of complex relations" (p. 63). Today we would regard this economy or polity of nature as a system in dynamic equilibrium; for as Darwin said, "in the long-run the forces are so nicely balanced, that the face of nature remains uniform for long periods of time" (p. 63). Yet, in "the case of a country undergoing some physical change, for instance, of climate. The proportional numbers of its inhabitants would almost immediately undergo a change" (p. 70). Or, as Darwin had expressed himself in his first sketch of his species theory, the essay of 1842, "let any singular change of climate ⟨occur⟩ here(?), how astoundingly some tribes (?) increase . . . the pressure is always ready . . . a thousand wedges are being forced into the oeconomy of nature" (1842–1844, pp. 7–8).

The economy of nature has places or stations which are involved in the struggle for existence and natural selection; "for as all organic beings are striving, it may be said, to seize on each place in the economy of nature, if any one species does not become modified and improved in a corresponding degree with its competitors, it will soon be exterminated" (1859, p. 87). Here Darwin developed an idea he had expressed in writing about coral reefs (1842), that "no station capable of supporting life is lost . . . there is a struggle for each station, between the different orders of nature" (p. 62). But on the other hand, "the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely

diversified places in the polity of nature, and so be enabled to increase in numbers" (*Origin*, p. 98). Darwin explained adaptation to the environment, both living and non-living, in writing that "the expression of conditions of existence, so often insisted on by the illustrious Cuvier, is fully embraced by the principle of natural selection. For natural selection acts by . . . adapting the varying parts of each being to its organic and inorganic conditions of life. . . ." (pp. 176–77; see Cuvier, 1817, p. 6; 1835, pp. 50, 53).

To proceed as we have done, by considering selected ecological concepts taken from Darwin's presentation of his views on the origin of species, admittedly ignores Darwin's emphasis and the original sequence of his ideas, but it does not do any violence to his perception of biological problems and relationships. We may summarize our findings as follows: Darwin's most fundamental ecological concept was that of the economics and sociology of organisms as a system—the economy or polity of nature. Within this system occur places in the economy of nature open to different organisms according to their habits of life and to their specific adaptation to the conditions of existence. We can let Darwin conclude in the terms which seem to have been most influential on Haeckel: "Let it be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life" (1859, p. 69; cf. pp. 3, 95, 115, 267).

HAECKEL AND ECOLOGY

If we turn to Haeckel's discussion of ecology in his "Darwin-Buch," his *Generelle Morphologie* (see Haeckel, 1852–1919, p. 67) we find that not only are reflections of these statements of Darwin clearly discernible, but also this topic occurs as a logical part of the discussion of the theory of evolution and the theory of natural selection. The association with Darwin could scarcely be closer.

When Haeckel introduced ecology, he discussed it as an area of biology and classified it as one aspect of the physiology of relationships, but he did not define it in any cut and dried fashion. Thus in different parts of his two volumes the emphasis shifts and different aspects of the field are stressed. The term ecology first appeared in a footnote on page eight of the first volume. Here Haeckel introduced it as a substitute for an arbitrarily restricted usage of the term "biology" and explained ecology as the science of the economy, of the habits, of the external relations of organisms to each other, etc. "—Oecologie . . . der Wissenschaft von der Oeconomie, von der Lebensweise, von der äusseren Lebensbeziehungen der Organismen zu einander etc." Only hundreds of pages farther on, in the latter part of his second volume when he came to discuss Darwin's concept of evolution and of natural selection, did Haeckel begin to present a fuller consideration of the term. First he discussed it briefly as the science of the economy of nature, of the mutual relations of organisms; and he described Darwin's cats-to-clover chain as an illustration (II, pp. 235–36). Then fifty pages later he presented the following formal account:

Ecology and Chorology

In the preceding sections we have pointed out repeatedly that without the theory of evolution all the big general series of phenomena of organic nature remain completely incomprehensible and inexplicable riddles, while by means of this theory they can be explained simply and consistently.(1) This holds especially true for two complexes of biological phenomena which we now in conclusion wish to single out in a few words. These form the subject of two special branches of physiology which so far have been largely neglected, namely, the ecology and chorology of organisms.(2)

[Haeckel's notes] (1) This tremendous mechanico-causal significance of the evolution theory for all biology, and in particular for the morphology of organisms, cannot often enough nor insistently enough be held up before its unthinking or blindly dualistic opponents, whose teleological dogmatism retains its strength only because they cannot elucidate these big general series of the phenomena of organic nature at all.

(2) οἶκος, ὁ household or housekeeping, living relations; Χώρα, ἡ dwelling place, distributional area.

By ecology, we mean the whole science of the relations of the organism to the environment including, in the broad sense, all the "conditions of existence." These are partly organic, partly inorganic in nature; both, as we have shown, are of the greatest significance for the form of organisms, for they force them to become adapted. Among the inorganic conditions of existence to which every organism must adapt itself belong, first of all, the physical and chemical properties of its habitat, the climate (light, warmth, atmospheric conditions of humidity and electricity), the inorganic nutrients, nature of the water and of the soil etc.

As organic conditions of existence we consider the entire relations of the organism to all other organisms with which it comes into contact, and of which most contribute either to its advantage or its harm. Each organism has among the other organisms its friends and its enemies, those which favor its existence and those which harm it. The organisms which serve as organic foodstuff for others or which live upon them as

parasites also belong in this category of organic conditions of existence. In our discussion of the theory of selection we have shown what enormous importance all these adaptive relations have for the entire formation of organisms, and specially how the organic conditions of existence exert a much more profound transforming action on organisms than do the inorganic. The extraordinary significance of these relations does not correspond in the least to their scientific treatment, however. So far physiology, [the science] to which this belongs, has, in the most one sided fashion, almost exclusively investigated the conserving functions of organisms (preservation of the individual and the species, nutrition, and reproduction), and among the functions of relationship [it has investigated] merely those which are produced by the relations of single parts of the organism to each other and to the whole. On the other hand, physiology has largely neglected the relations of the organism to the environment, the place each organism takes in the household of nature, in the economy of all nature, and has abandoned the gathering of the relevant facts to an uncritical "natural history," without making an attempt to explain them mechanistically.

This great gap in physiology will now be completely filled by the theory of selection and the theory of evolution which results directly from it. It shows us how all the infinitely complicated relations in which each organism occurs in relation to the environment, how the steady reciprocal action between it and all the organic and inorganic conditions of existence are not the premeditated arrangements of a Creator fashioning nature according to a plan but are the necessary effects of existing matter with its inalienable properties and their continual motion in time and space. Thus the theory of evolution explains the housekeeping relations of organisms mechanistically as the necessary consequences of effectual causes and so forms the monistic groundwork of ecology. Now just the same thing also holds true for the chorology of organisms. . . .

(Haeckel, 1866, II, pp. 286–87)

[Throughout this translation I have departed from a literal rendering to the extent that seems necessary to produce clear and tolerable English. I have translated Haeckel's phrase *Descendenz-Theorie* as "theory of evolution" because Haeckel had already equated these expressions on p. 148 of Vol. II. We can justify translating *Naturhaushalt* as "economy of nature," for in the German translation of the *Origin of Species* used by Haeckel, H. G. Bronn used *Haushalt der Natur* or *Natur-Haushalt* as equivalents for Darwin's "economy of nature"—and for his "polity of nature," also. It is a pleasure to acknowledge the advice of Professor R.-M. S. Heffner, whose suggestions have been of great value in improving this translation.]

After 1866, Haeckel continued to make passing references to ecology. During the inaugural lecture in the philosophical faculty of Jena which he delivered in January 1869, he again discussed ecology in surveying the field of zoological science. Here he made the most quotable yet representative of his statements on its nature: "By ecology we mean the body of knowledge concerning the economy of nature—the investigation of the total relations of the animal both to its inorganic and to its organic environment; including, above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact—in a word, ecology is the study of all those complex interrelations referred to by Darwin as the conditions of the struggle for existence." (Although this translation, given on p. [v] in the *Principles of Animal Ecology* by W. C. Allee et al., is a free rather than a literal rendering, I consider it very faithful to Haeckel's meaning, and so I quote it as independent corroboration of my interpretation. For the original passage see Haeckel, 1869, p. 17; for a very literal translation see Haeckel, 1883, p. 200).

This account of ecology was given in the lecture of Haeckel's which was mentioned explicitly by John Scott Burdon-Sanderson in his presidential address to the British Association for the Advancement of Science (1893). And it was in this latter widely distributed address that Burdon-Sanderson publicized ecology by recognizing it as an aspect of biology equal in rank with physiology and morphology—and of these branches "by far the most attractive" (p. 465).

Three other brief references to ecology by Haeckel occurred in writings of his which were also translated into English and so are also involved in the history of the term in our own language. Of these, two were in popular books which each went through a number of editions in England and America: *The History of Creation* and *The Evolution of Man*, (see indexes under oecology or oekology). A third reference in English appeared in the translation of Haeckel's *Plankton-Studien* published in the Report of the U. S. Commissioner of Fish and Fisheries.

QUANTITATIVE METHODS

These *Plankton-Studien*, first published in 1890, offer us a revealing insight into Haeckel's understanding of ecological points of view. Here the significant aspect is Haeckel's attitude toward the efforts by Victor Hensen (1835–1924) of Kiel to

introduce quantitative methods into the study of marine biology in order to attack the problem of estimating the productivity of the sea. Even popular writing had mentioned the importance of foraminifera and diatoms in the economy of the sea for decades (Hartwig, 1861, chap. 17); the value of Hensen's approach lay in his aim to discover the order of magnitude of their role in food production.

As a first step toward this goal, Hensen planned to concentrate on the basic food-stuff such as the diatoms and copepods which form much of this assemblage of floating marine life for which he invented the term "plankton" (Hensen, 1887, p. 1). To make a start he boldly assumed for normal plankton distribution a uniformity which is still being debated (Hardy, 1955). It was on this assumption that he based his estimates of plankton populations for different areas; for he made these estimates by extrapolation from carefully counted samples. These samples were obtained by filtering a water column of a calculated cross-sectional area by making a vertical haul of his specially designed net. It was the counts of these samples which led Hensen to the unexpected conclusion that the quantity of plankton is greater in the colder waters of the northern seas than in the warmer waters of the tropics.

On the basis of his own collecting experience and his interpretation of the collections of the great Challenger Expedition (1872–1876), for which Haeckel had described the deep-sea medusae, the siphonophores, and the radiolaria, Haeckel did not hesitate to attack Hensen's methods and to question his aims. Part of the objections Haeckel raised against Hensen's assumptions of a uniform plankton distribution can easily be understood as due to skepticism based on personal experience, for Haeckel (1891a, pp. 308–18), like Darwin (1839, pp. 14–20; cf. pp. 189–90) and many other observers, had been struck by the appearance of dense local accumulations of plankton which even had visibly distinct boundaries. Here Haeckel seems to have been misled because he overrated the total effect of spectacular situations and underrated the inconspicuous conditions which proved to be statistically far more significant. But this involves a technical though most interesting controversy which can hardly be settled by nonspecialists. Another part of Haeckel's plausible arguments turns out to be based on misinterpretation of Hensen's procedure or his reasoning (cf. Hensen, 1891), and these can be dismissed as regrettable aspects of Haeckel's polemics. But the most revealing part of his objections involves his suspicion of quantitative studies as a matter of principle. "Statistics in general is well known to be a very hazardous science because it is usually employed to find the approximate average value of a magnitude from a number of imperfect observations" (Haeckel, 1891a, p. 322).

Haeckel had spoken of the economy of nature in 1866 when he was first discussing ecology, and in this discussion of planktology he cited as ecological problems "the interesting and involved vital relations of pelagic organisms, their habits of life and economy" (p. 250), but he could not appreciate Hensen's aim to make this study of the economy of the sea a quantitative one. He rejected Hensen's discovery of the great abundance of plankton in colder waters because it did not agree with his own subjective impressions and qualitative observations. Though he denied it, he was apparently misled in part by allowing his attention to be concentrated on the richness of the tropics in number of species as opposed to number of individuals (pp. 267, 303–308). In opposing Hensen's methods Haeckel argued that the employment of "exact or mathematical methods . . . unfortunately is impossible in most branches of science (particularly in biology), because the empirical foundations are much too imperfect and the present problems much too complicated. Mathematical treatment of these does more harm than good because it gives a deceptive semblance of certainty which is not actually attainable. Part of physiology also involves problems which are difficult or impossible to resolve exactly, and these include the chorology and ecology of plankton" (Haeckel, 1891a, p. 331).

In regard to the "metabolism of the sea" (Stoffwechsel des Oceans), Haeckel's criticism, if shrewd, was both partial and unhelpful when he remarked, "To me it seems wholly indifferent whether or not the number of these billions is indicated to us by quantitative plankton analysis. To understand their physiological significance, it would be more important to determine the speed of their increase" (p. 329). Haeckel continued with a few general comments favoring a subjective evaluation of this "metabolic" cycle, and then he concluded by suggesting with greater enthusiasm that "the watery transparency of the pelagic fauna, the periodic appearance of many pelagic organisms in

swarms, their abundant accumulation in 'zoöcurrents,' their relation to ocean currents in general, are only a few of the many great problems which planktology offers to the research impulse of man" (p. 334). In the whole plankton controversy, while Haeckel may have been correct in important matters of detail, he persistently obscured the potential value inherent in Hensen's program.

But it is time to contrast Haeckel's suspicion of Hensen's quantitative methods in plankton studies with Darwin's approval and use of Hensen's analogous methods in ecological studies on the earthworm. In his work on *The Formation of Vegetable Mould through the Action of Worms* (1881), Darwin was interested in estimating the weight of soil per acre brought to the surface each year by earthworms. For this he praised Hensen's "admirable paper" on the problem, and he did not hesitate to extrapolate from measurements based on a few yard-square sample areas. In regard to skepticism concerning his conclusions Darwin simply observed: "Here we have an instance of that inability to sum up the effects of a continually recurrent cause, which has often retarded the progress of science, as formerly in the case of geology, and more recently in that of the principle of evolution" (quotations are from the end of Darwin's Introduction).

CONCLUSION

Haeckel's original presentation of the term "ecology" in 1866 embodies concepts that come straight from the *Origin of Species*. His contribution to the science of ecology was made in his role of academic spokesman for Darwin; it was to mark out this area of biology as a scientific entity and to provide it with an effective name happily reminiscent of the older concept of the economy of nature—one of the many fruitful ideas which illuminate the pages of the *Origin of Species*. In contrast to Darwin's appreciation of the potential value of quantitative studies as a means of understanding the dynamics of ecological relations, Haeckel's distrust of quantitative studies seems static and unexpectedly conservative. As a source for a vital stimulus to the continuing development of ecology we must look rather to the work of Charles Darwin.

LIST OF LITERATURE

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, and KARL P. SCHMIDT. 1949. *Principles of Animal Ecology*. Saunders, Philadelphia.

BURDON-SANDERSON, JOHN S. 1893. Inaugural Address. *Nature, Lond.*, 48: 464–72. Also in *Rep. Brit. Ass.*, 1893: 3–31; *Rep. Smithson. Instn*, 1893: 435–63.

CUVIER, GEORGES. 1817. *Le Règne animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Vol. 1, Paris.

——. 1835. *Leçons d'anatomie comparée*. 2nd ed. Vol. 1, Crochard, Paris.

DARWIN, CHARLES. 1839. *Journal of Researches into the Geology and Natural History of the various countries visited by H. M. S. Beagle*. . . . Henry Colburn, London. [Facsim. reprint. Hafner, New York, 1952.]

——. 1842. *The Structure and Distribution of Coral Reefs*. [Reissued in *Geological Observations*. . . , 1851], London.

——. 1842–1844. *The Foundations of the Origin of Species: two essays written in 1842 and 1844*. Edited by Francis Darwin. Cambridge University Press, Cambridge, 1909.

——. 1859. *On the Origin of Species by Means of Natural Selection, or the preservation of favoured races in the struggle for life*. (A reprint of the first edition). Watts, London, [1950]. I have verified the quotations in the first edition, but have given page references to the more available reprint edition.

——. 1860. *Über die Entstehung der Arten*. . . . Translated by H. G. Bronn. Schweizerbart, Stuttgart. For each of the passages quoted I have checked Bronn's translation and have found it reliable.

——. 1881. *The Formation of Vegetable Mould, through the Action of Worms, with Observations of their Habits*. London.

HAECKEL, ERNST. 1852–1856. *The Story of the development of a youth* . . . *Letters to his Parents, 1852–1856*. Translated by G. B. Gifford. Harper, New York, 1923.

——. 1852–1919. *Ernst Haeckel: Forscher, Künstler, Mensch. Briefe*. . . . Edited by George Uschmann. Urania, Jena, 1954.

——. 1862. *Die Radiolarien*. Reimer, Berlin.

——. 1863. Ueber die Entwickelungstheorie Darwin's. [In *Gesammelte populäre Vorträge aus dem Gebiete der Entwickelungslehre*. Heft 1. 1878.] Strauss, Bonn.

——. 1866. *Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie*. 2 vols. Reimer, Berlin.

HAECKEL, ERNST. 1869. Ueber Entwickelungsgang und Aufgabe der Zoologie. [In *Gesammelte populäre Vorträge aus dem Gebiete der Entwickelungslehre.* Heft 2. 1879.] Strauss, Bonn.

——. 1873. Author's preface to the English edition. [In *The History of Creation.* Vol. 1. 1887.] Appleton, New York.

——. 1874. Aus einer autobiographischen Skizze vom Jahre 1874. [In *Himmelhoch Jauchzend . . . Erinnerungen und Briefe der Liebe.* Edited by Heinrich Schmidt, 1927]. Reissner, Dresden.

——. 1875. *The History of Creation.* Translated by L. D. Schmitz; revised by E. R. Lankester. 2 vols., London.

——. 1879. *The Evolution of Man: a popular exposition of the principal points of human ontogeny and phylogeny.* 2 vols. Kegan Paul, London.

——. 1883. *The Pedigree of Man: and other essays . . . .* Translation [of *Gesammelte populäre Vorträge*] by E. B. Aveling. Freethought Publishing Company, London. International Library of Science and Freethought, Vol. 6.

——. 1890. *Plankton-Studien. Vergleichende Untersuchungen über die Bedeutung und Zussammensetzung der pelagischen Fauna und Flora.* G. Fischer, Jena.

——. 1891a. Plankton-Studien. *Jena. Z. Naturw.*, 25: 232–336.

——. 1891b. Planktonic Studies: a comparative investigation of the importance and constitution of the pelagic fauna and flora. Translated by G. W. Field, *Rep. U. S. Comm. Fish.*, 1889–1891: 565–641.

HARDY, A. C. 1955. A further example of the patchiness of plankton distribution. Pp. 7–11 in *Papers in Marine Biology and Oceanography.* Supp. to Vol. 3 of *Deep Sea Research.* London.

HARTWIG, G. 1861. *The Sea and its Living Wonders.* Translated from the fourth German edition and partly rewritten by the author. 2nd ed. Longmans, Green, London.

HENSEN, VICTOR. 1887. Ueber die Bestimmung des Planktons oder des im Meere treibenden Materials an Pflanzen und Thieren. *Wiss. Meeresuntersuch.*, 5: 1–107.

——. 1891. *Die Plankton-Expedition und Haeckel's Darwinismus. Ueber einige Aufgaben und Ziele der beschreibenden Naturwissenschaften.* Lipsius & Tischer, Kiel.

JACKSON, B. DAYDON. 1913. Authorship in the *Amoenitates Academicae* [of Carl Linneaus, 1749–90]. *J. Bot., Lond.*, 51: 101–103, 224.

KLAAUW, C. J. VAN DER. 1936. Zur Geschichte der Definitionen der Oekologie, besonders auf Grund der Systeme der zoologischen Disziplinen. *Sudhoffs Arch. Gesch. Med.*, 29: 136–77.

——. 1951. Qu'est-ce que l'écologie? *Ann. biol.*, 27: 103–15.

LINNÉ, CARL VON, *praeses.* 1749. *. . . Specimen academicum de oeconomia naturae . . . .* Diss. Upsala (I. J. Biberg respondent). [Also in Linné's *Amoenitates academicae*, Vol. 2 (1751), pp. 1–58.]

——, *praeses.* 1749. I. J. Biberg, respondent. The oeconomy of nature, pp. 39–129 in *Miscellaneous tracts relating to natural history, husbandry and physick, translated from the Latin* [*of the Amoenitates Academicae*] with notes by B. Stillingfleet. 2nd ed. London, 1762.

——, *praeses.* 1760. *. . . Dissertatio academica de politia naturae.* Diss. Upsala (H. C. D. Wilcke, respondent). [Also in Linné's *Amoenitates Academicae*, Vol. 6, 1763, pp. 17–39.]

——, *praeses.* 1760. H. C. D. Wilcke, respondent, "On the police of nature," pp. 129–64 in Select Dissertations from the *Amoenitates Academicae*, a supplement to Mr. Stillingfleet's *Tracts relating to Natural History*, translated by F. J. Brand. Vol. 1. London, 1781.

MCATEE, W. L. 1947. The Cats-to-Clover Chain. *Sci. Monthly*, 65: 241–42.

SEARS, PAUL B. 1950. *Charles Darwin. The Naturalist as a Cultural Force.* Scribners, New York.

THE DEVELOPMENT OF PEAT LANDS

By EVILLE GORHAM

Freshwater Biological Association, Ambleside, England

INTRODUCTION

MOORLANDS, bogs, and fens are familiar features of the landscape in temperate and subpolar parts of the world, and the problems of their origin and development are of great scientific as well as practical interest. Reclamation of such land, and use of the peat itself, is a matter of importance throughout northern Europe, and for this reason, if no other, it is highly desirable to know something of the processes involved in peat accumulation, and of the factors controlling it.

Since the study of peat lands entails dealing with a mass of complex relations between organisms and their environments, our understanding of them is necessarily fragmentary and far from complete. Nevertheless, if a brief outline is presented of one type of vegetation and soil sequence which occurs in many parts of northern Britain, the scene may be set for a consideration of the way in which variations in the major environmental factors—climate, geology, relief, and organisms—can modify this type of succession over long periods of time, in different parts of the world. First, however, it would be well to point out that our knowledge of bog development is not wholly a result of modern science, but is based upon careful observation and accurate interpretation by a number of amateur naturalists and agriculturists, who laid the groundwork for our present theories long before the study of nature became largely the preserve of the professional scientist.

EARLY INVESTIGATIONS

Peat lands have been studied for a long time, and a great deal has been known about them since the early years of the nineteenth century (Gorham, 1953a). As long ago as 1652, Gerard Boate classified several types of Irish bogs, and in 1685 William King described their development, clearly apprehending the changes in plant communities which accompanied peat accumulation. Linnaeus, in his travel journals of the mid-eighteenth century, provided notes on the flora of bogs, and on the origin of the hummocks which characterize their surfaces.

During the first years of the nineteenth century, the study of peat lands increased enormously in response to new demands for agricultural expansion. De Luc in Germany and Aiton in Scotland described the way in which lakes became filled with peat and changed into fens or bogs, and accompanied their discussions by lists of plants typical of the successive stages. Aiton also classified the main types of Scottish peat lands, and gave lists of their common plants. The importance of topography to bog formation and development was appreciated, as was the influence of chemical factors. Regarding the latter, the Scottish clergyman Rennie ascribed peat formation to retardation of decomposition by waterlogging, owing to (1) absence of oxygen, (2) low temperature, (3) lack of fluctuation in moisture and temperature, and (4) the presence, in various plants, of an antiseptic principle giving rise to peat. This antiseptic principle was considered to be possibly connected with organic or mineral acids, methane or sulphuretted hydrogen, bitumens, iron sulfate, or perhaps merely mechanical structure of the peaty materials, and their lack of inorganic minerals.

A notable accomplishment of the other chief Scottish investigator, William Aiton, was his recognition of the cyclical alternation of dry hummocks and wet hollows in the growth of raised bogs, responsible for the mosaic distribution over the bog surface of different plants characteristic of the wet and dry phases. This author also wrote of erosion as the natural culmination of bog development, a view favored by many modern workers both here and on the European continent.

The concept of plants as indicators of environmental conditions was put forward during this

period, and Rennie expressed the opinion that by determining the plants in the various strata of a peat deposit one might ascertain the conditions in the bog at the time the peat was laid down. It was also suggested that peat formed during dry seasons could be distinguished from that laid down in wet periods, since the growth of many bog species which yielded different kinds of peat was dependent upon weather conditions.

One attractive hypothesis of these early days has had to be discarded. Early Dutch naturalists had claimed that a peat bog was a living, growing organism, and that the surface vegetation merely grew upon its dead outer skin. Although recognized as outmoded by most later investigators, this view was strongly championed as late as 1794 by Doctor Anderson of Aberdeenshire. It was equally strongly opposed by Rennie, who would "dismiss this new species of vegetable from the list of plants, till its habits and qualities are distinctly ascertained. I would only suggest, that of all devouring monsters it must be the most dreadful, according to the Doctor's account; for, as I shall show, ploughed fields, large trees, loaded boats, men and women, and the largest animals, houses, nay, streets and whole cities, have been swallowed up in its all-devouring jaws."

A COMMON TYPE OF BOG DEVELOPMENT

Extensive peat deposition occurs chiefly in waterlogged habitats. While dry acid humus may occasionally pile up to a height of as much as a foot or so over certain kinds of well-drained forest soil under conifers (Romell and Heiberg, 1931), only wet fens and bogs can amass great thicknesses of peat, quite commonly to a depth of fifteen feet, and of more than thirty feet in exceptional circumstances. In waterlogged soils the circulation of air may become greatly restricted, and the store of oxygen severely depleted, often to vanishing point (Malmström, 1923; Pearsall, 1938; Carter, no date). As a result, dead plant residues which are continually being produced by the vegetation decompose less rapidly than usual, and peat begins to accumulate. The rate of decay of celluloses and hemicelluloses may be especially slow in the case of the bog moss *Sphagnum*, which grows most abundantly in acid sites where nutrients such as phosphorus and lime are scarce (Waksman, 1936, 1942), and where cellulose-decomposing organisms are scarce (Waksman and Stevens, 1929). Thus a deficiency of nutrients in the soil commonly favors peat formation.

If the climate is extremely wet (in the British Isles and southern Scandinavia for instance, wherever rainfall exceeds about one hundred centimeters per year), peats may develop even on gentle slopes, and on plateau soils not originally submerged (Granlund, 1932; Pearsall, 1950; Barry, 1954). In certain circumstances, acid peat may form on such upland soils even when they are relatively rich in lime (Webb, 1947). For if the atmosphere is sufficiently humid, and precipitation exceeds evaporation at all seasons, some species of the bog moss *Sphagnum* may grow where the ground is not saturated. And if rainfall is high, even fairly rich soils may be leached of nutrients at the surface, thus creating favorable conditions for the establishment of the bog mosses, and unsuitable conditions for the rapid breakdown of their dead residues. On poorer flat lands there is also the possibility that leaching can lead to formation of an impermeable iron pan in the subsoil, and hence to waterlogging and bog invasion (Pearsall, 1950). However, bog advance up sloping ground is probably most commonly due to damming up of the water table by peat accumulation, as described by Malmström (1923, 1931) for north Swedish bogs, and by Millington (1954) for bogs in Australia.

Northern Britain, with its very high annual rainfall, is a most suitable area in which to study bog development. Frequently, if one views a peat cutting at the side of a big bog, there is to be seen at the very base—just above the underlying clay—a layer of peat formed by the common reed *Phragmites communis*, which usually grows along lake shores. Then may occur a horizon of rather highly decomposed sedge peat, and one of brushwood remains, with a very characteristic coarse, twiggy texture. On top are found thick deposits of the bog moss *Sphagnum*, in varying degrees of decay, with interposed horizons of heather and cotton grass remains, and sometimes zones with numerous buried pine stumps. In some instances thick deposits of lake muds, with a soft gelatinous texture due to highly decayed organic matter, occur above the basal clay, and bear witness to the original presence of a lake basin.

The vertical succession just described is paralleled by the horizontal zonation to be observed at the shores of many lakes today. Reeds (*Phragmites*), cattails (*Schoenoplectus*), and reed-mace (*Typha*) fringe the shore and advance into shallow water. Behind this reed swamp may be seen a band of sedge meadow with different species of *Carex* (depending upon soil conditions), or in more

silted localities a grass meadow with plants such as the reed grasses (*Phalaris arundinacea* and *Calamagrostis canescens*). These fen meadows in turn are encroached on by alder and willow bushes; these grow up to form a closed-canopy fen woodland termed "carr," which may persist for a long time. Eventually, however, under a wet climate, species of the bog moss (*Sphagnum*), together with purple moor grass (*Molinia caerulea*) and sweet gale (*Myrica gale*), invade the carr, and the trees gradually die off. Then if atmospheric humidity is sufficient, the bog moss grows above the level of the ground water table, and begins to form what is known as a "raised bog" because of the convexity it exhibits when seen in side view. Such bogs, whose surfaces are completely removed from the influence of water from the mineral soil, are called "ombrogenous."

While this normal British picture of bog succession is paralleled in many other regions, geological factors may almost entirely suppress the earlier phases in certain habitats. For example, on the flat and heavily glaciated granites of northeastern North America, the hardness of the rock and its poverty in easily soluble plant nutrients may sometimes permit *Sphagnum* bogs to be established directly in the smaller and shallower of the wet rock hollows, so that there is very little zonation apparent in their peat deposits, except perhaps for a predominance of the more aquatic *Sphagnum* species in the early stages (Nichols, 1918). However, where the basins are large enough to allow a moderate degree of silting, a more normal reed-swamp–sedge-meadow–bog succession is commonly observed.

It may be desirable at this stage to point out the complexity of peat-land terminology (cf. Waksman, 1942). The Uppsala school of Swedish ecologists regard "bog" as applying solely to ombrogenous raised or blanket-bog habitats; all others are various types of "fen" (Du Rietz, 1949; Sjörs, 1950a). In England, however, Pearsall (1938, 1950; Gorham and Pearsall, 1956a) has designated the stage transitional to ombrogenous bog as "lacustrine bog," in which some mineral soil-water influence is still felt. And in drier parts of Britain where ombrogenous bog is unable to develop, complexes of reed swamp, sedge fen, carr, and *Molinia–Myrica–Sphagnum* communities are often termed "valley bogs" (Tansley, 1939; Newbould and Gorham, 1956). This usage has also been adopted by Kulczynski (1949) for Polish peat lands.

Raised bogs are enabled to build up because of the marked capacity of *Sphagnum* to hold water, and hence to retard percolation. This moss serves as a very efficient sponge, and many bog peats contain ten to twenty times their own weight of water. The percolation of rain water through the peat is also much retarded by highly decayed horizons commonly found deep down in most bogs. The water balance of the bog is thus buffered to a marked degree against periods of either heavy rain or drought, and bog surfaces may rise and fall appreciably during such periods (Kulczynski, 1949). The convexity of the raised bog is probably due at least partially to the inhibition of lateral extension by nutrient-rich waters from the surrounding mineral soils, these being unsuitable for the growth of most raised-bog *Sphagna* (Godwin, 1946), and favoring the rapid breakdown of dead vegetable remains. The more extreme fluctuations of water in the marginal areas may also be of much importance (Kulczynski, 1949).

Some of the species of *Sphagnum* which invade willow carr and characterize incipient raised bog development, may be replaced in the mature stages by others of the same genus. For example, *Sphagnum recurvum*, *S. teres*, and *S. subsecundum* may give way to *S. cuspidatum*, *S. rubellum*, *S. magellanicum*, and *S. fuscum*. One species, however, *Sphagnum papillosum*, is common throughout.

Chief among the higher plants accompanying the bog moss on ombrogenous West European bogs are heather (*Calluna vulgaris*), cross-leaved heath (*Erica tetralix*), cotton grasses (*Eriophorum* species), deer grass (*Trichophorum caespitosum*), white beak sedge (*Rhynchospora alba*), sundews (*Drosera* species), bog asphodel (*Narthecium ossifragum*), cranberry (*Oxycoccus* species), cloudberry (*Rubus chamaemorus*), and bog rosemary (*Andromeda polifolia*). There is in addition a host of bryophytes and microscopic algae.

The course of raised bog formation has been pictured as a lenticular "regeneration complex" of hummock and hollow alternation, the cyclical mode of development being generally ascribed to the different ecological requirements of the various species of *Sphagnum* (von Post and Sernander, 1910; Osvald, 1923; Tansley, 1939). *S. cuspidatum*, for example, favors water-filled depressions on the bog, and grows so successfully as to obliterate them, thus providing conditions suitable for other species, such as *S. papillosum*, *S. magellanicum*, and *S. tenellum*. When these have built up a low cushion of peat, still other species invade, *S. rubellum*, *S. fuscum*, and perhaps *S. imbricatum*. These build

the hummock still higher, until finally the top dries out enough to permit lichens and liverworts to overgrow it, and upward growth ceases to exceed the rate of decay. In some cases erosion may also set in at this stage. Once the hummock stops growing, it is liable to be overtaken by the development of similar hummocks in the surrounding pools, which eventually overtop it and make it into a new pool. This becomes water-filled, and is colonized by *Sphagnum cuspidatum*, whereupon the cycle starts anew. Tolpa (1947) has claimed that lenticular regeneration is characteristic of Atlantic climates without a marked summer water-deficit, continental climates producing floristically uniform peat strata.

Other species of bog plants also show preferences for either hummocks or hollows. In Britain, heather (*Calluna vulgaris*), the cotton grass *Eriophorum vaginatum*, and the lichens (*Cladonia* species) are among the plants typical of the former, while the white beak sedge (*Rhynchospora alba*), another cotton grass (*Eriophorum angustifolium*), and the alga *Zygogonium ericetorum* (which forms a purplish skin on many dried-out pools), are plants more commonly abundant in hollows.

Where the bog surface is not entirely flat, the hummocks and hollows tend to be elongated at right angles to the slope, with the hummocks forming a network in the meshes of which the hollows are interspersed. Such formations are common not only in bogs and fens lying upon sloping ground, but also in the concentrically domed, raised bogs of flat land (Sjörs, 1948). In the case of some British bogs on gentle slopes, it has been suggested that pressure ridges are set up at certain points in the peat mass, owing to its fluidity and tendency to flow downslope (Pearsall, 1956). Tears in that part of the surface peat under tension are also invoked to explain some types of bog pool, and desiccation effects may intensify the above developments. On flat ground, however, where the classic, concentric raised bogs are found, interpretations based on pressure ridges, or wrinkling due to desiccation, would seem to be at variance with the theory of lenticular regeneration.

An extraordinary type of hummock-hollow development, which will have to be comprehended in any inclusive theory of their origin, is that exemplified by Hammarmossen in north Sweden, a concentrically domed bog on a sandy and very flat riverine plain, described in some detail by Granlund (1932) and also by Sjörs (1948), who has published an excellent aerial photograph. This bog, like many others, exhibits a very marked pattern of hummocks interspersed with large hollows, elongated at right angles to the slope; but instead of the hollows being the usual shallow surface pools, they extend right down to the thin basal layer of impervious peaty mud more than three meters beneath the present bog surface. Yet another form of bog development, common in the British Isles, requires elucidation too. It is the type of rather flat or slightly convex blanket bog with little or no hummock-and-hollow pattern, but with occasional large *Sphagnum*, *Rhacomitrium*, or *Leucobryum* hummocks scattered apparently at random over the bog plane. Even in more normal bogs, the hypothesis of lenticular regeneration fails to account for the regular elongate pattern of hummocks and hollows following the contour. It is understandable that pools are unlikely to be extended in any direction other than at right angles to the slope—self-drainage would result—but it is not clear why there should be any elongation at all, instead of a series of small circular pools, for example. Perhaps erosive forces do tend to bring about extension in all directions, with only those pools in which it takes place at right angles to the slope being able to persist. The whole matter of hummock-hollow regeneration appears greatly in need of further study, preferably with the cooperation of students trained in the physical sciences.

The horizontal zonation mentioned earlier is related to the vertical layering in bogs through the fact that the zones are seldom stationary over long periods. As silting of a lake basin proceeds it becomes shallower, and the addition of vegetable debris from within and without the lake accelerates the filling in, hence the depths of standing water continually decrease. Because of this the reeds of the shore move outward into deeper water, by means of their creeping rootstocks. They are replaced by the sedges, which are better suited to the newly shallowed bottom than are the reeds. Once silting and peat deposition have raised the level of the bottom to that of the standing water, alder and willow bushes can invade the sedge fen, and a carr woodland may develop over the older sedge and reed remains. The carr in turn gives way in wet climates to lacustrine bog with *Sphagnum–Molinia–Myrica* communities (Pearsall, 1938), and these may finally be replaced by raised bog species forming deep peat well above the level of the old lake. In this way, partly through the physical phenomenon of silting, and partly because of the intrinsic biological factor of peat accumulation, a

horizontal series of plant communities may give rise to a vertical sequence of peat types with very different characteristics.

Of course one seldom, if ever, sees the whole vertical sequence to raised bog laid out around a lake basin. However, at Esthwaite Water in the English Lake District, Professor W. H. Pearsall has described the entire succession up to the invasion of willow carr by *Sphagnum*, and the formation of a *Sphagnum–Molinia–Myrica* community along its edge (see Tansley, 1939). Examples of raised bogs showing typical vertical profiles, though now unfortunately much altered at the surface through draining and burning, are also to be found in the Lake District, for example at Rusland and along the Leven estuary. However, the best of British ombrogenous bogs, in their natural state, are now to be found in Ireland and Scotland. Professor Pearsall has recently investigated a particularly interesting series in Sutherland (Pearsall, 1956), which appears to show many features reminiscent of Scandinavian bogs.

The productive capacity of bogs and fens in their natural state is largely unknown, although their agricultural potential has frequently been investigated. A preliminary attempt to gain some information upon this point has indicated that over a wide range of vegetation types characteristic of wet habitats in Britain, the autumn standing crops are usually between about 4,000 and 14,000 kilograms per hectare (Pearsall and Gorham, 1956). These figures in general resemble those for similar vegetation types on dry land, and compare with an average annual leaf fall of about 3500 kilograms per hectare in British woodland communities (Ovington, 1956). Within the above range, the higher standing crops tend to occur on the less acid soils receiving a greater mineral supply; but such soils do not, however, invariably produce large standing crops. For the reed *Phragmites communis* there is some tentative evidence to suggest that shoot size and percentage of flowering shoots are to some extent dependent upon the degree of silting of the habitat (Gorham and Pearsall, 1956b).

A last point to be made in this account of bog succession is the astonishing ability of some plants to persist in unfavorable habitats, and so to exhibit what may be described as "biological inertia." That is, once having colonized an area, they may continue to exist there long after the conditions suitable for their establishment have disappeared. For instance, in many areas being transformed from sedge fen into *Sphagnum* bog, the sedges remain for a long time pushing through the moss cushions—surviving by virtue of having their roots in the richer peat, or sometimes the moving ground water, beneath (Du Rietz, 1949). Similarly, around the edges of many small pine bogs filling granite hollows in parts of Fennoscandia, the reed *Phragmites* persists in a dwarfed and sterile state under conditions of acidity and nutrient impoverishment far too severe for its establishment. It is presumably a relic of the time, centuries ago, when the bogs were shallow ponds and lakes, and the marginal soils much richer and less acid (Auer, 1923; Gorham, 1950).

CHEMICAL ASPECTS

The type of bog development outlined above involves considerable chemical change, not only in the composition of the waters reaching the peat surfaces, but also in the peats formed at various stages, and in the plants from which the peats originate. These changes are most clearly marked at the point when the bog becomes ombrogenous, i.e., when the surface ceases to be influenced by water which has percolated through mineral soil, and obtains its entire supply of moisture by atmospheric precipitation. While bog successions are much too slow to be observed directly, one can often make reasonable assumptions about their chemical consequences, by observing the differences between bogs which have developed at somewhat different rates, so that they are at present in different stages of growth. Undoubtedly such a method should be applied with caution, but at least some qualitative differences may be fairly well established.

The initial composition of rain water, and its composition after percolation through mineral soil materials, differ profoundly. In northern Britain, the dissolved ions of rain are predominantly either sodium chloride, derived from sea spray and brought in by westerly winds, or sulfuric acid originating from industrial atmospheric pollution, and coming chiefly from the south and east (Gorham, 1955a). The surface waters of bogs fed solely by rain often closely resemble it in composition (Gorham, 1956b). On the other hand, in percolating through rocks and soil minerals, rain picks up a good deal of calcium and magnesium bicarbonate, along with some other salts (Gorham, 1956a; Mackereth, Lund, and Macan, Proc. Linn. Soc., 1957 in press). Calcium bicarbonate accounts for the major proportion of the ions dissolved in min-

eral soil waters (cf. Witting, 1947, 1948; Gorham, 1955b, 1956a), and owing to this, their acidity is seldom very high. In northern Britain, it appears that as long as some mineral soil water reaches the peat, its acidity does not become very great, and peat *p*H generally remains above 4.5 (Gorham, 1953b). In contrast, ombrogenous bogs exhibit quite high acidities, with *p*H values generally below ombrogenous bog waters in Britain is almost entirely due to free sulfuric acid. While colloidal organic acids ("humic acids") are also abundant—as shown by the high levels of adsorbed and exchangeable hydrogen ions in the peat (Gorham, 1953b, c)—they are probably only slightly dissociated in the presence of strong mineral acid.

Where the water supply has percolated through

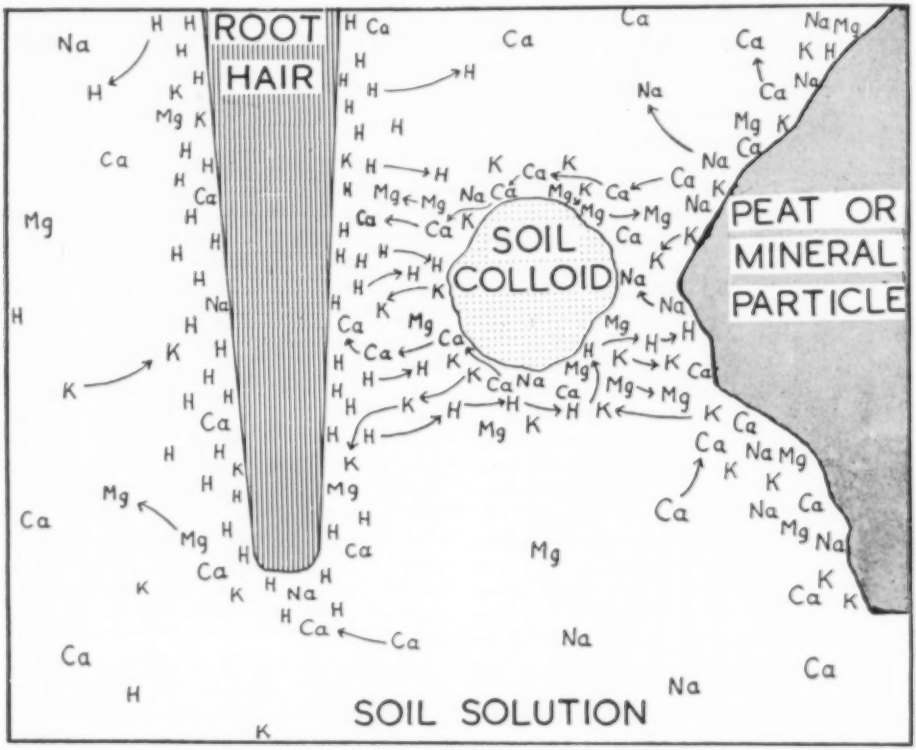

FIG. 1. CONTACT EXCHANGE OF ADSORBED IONS BETWEEN ROOTS AND SOILS (After Keller and Frederickson, 1952). Explanation in text.

4.2, and with occasional rather dry peat samples below 3.0. In extremely dry weather, bog waters may show exceptionally high levels of both acidity and metal cations, owing to oxidation of hydrogen sulfide produced from organic sulfur compounds in the peat. This hydrogen sulfide oxidizes to sulfuric acid, and some of the hydrogen ions of the acid exchange for metal cations adsorbed on the peat colloids, which then appear free in solution (Gorham, 1956b).

It seems likely that the high acidity of most mineral soils, the colloidal adsorptive complexes of the peat are largely saturated by swarms of metallic cations at their surfaces—chiefly calcium, magnesium, potassium, and sodium (see Fig. 1)—while in ombrogenous peats, hydrogen may account for most of the adsorbed cations (Gorham, 1953b; Malmer and Sjörs, 1955). Among the metallic cations, Swedish workers have recently demonstrated a shift from calcium to magnesium as the major adsorbed component, in passing from poor fens flushed by mineral soil water to highly acid

bogs wholly dependent upon rain for their surface water (Malmer and Sjörs, 1955; see also Mattson, Sandberg, and Terning, 1944). The magnesium and sodium in both the peats and waters of the latter sites probably derive mainly from sea spray (cf. Gorham, 1955a, 1956b). The way in which sea spray gets into the atmosphere, and eventually supplies chlorides of sodium and magnesium to rain and bog waters, is probably as follows. High winds develop high waves on the sea surface, and above a certain height these tend to break and form foam patches, made up of myriads of small bubbles. Similar foam patches may be formed by waves breaking on beaches (Boyce, 1951). When these bubbles rise to the surface and burst, they throw up tiny jets, which break off minute droplets—often sufficiently small to be carried up into the air and evaporated. The tiny particles thus formed act as nuclei for the condensation of raindrops, and are brought to the ground with the rain (Woodcock et al., 1953). They are also probably caught by vegetation (Sugawara, Oana, and Koyama, 1949; Eriksson, 1955).

The amount of adsorbed metallic cations in peat may be of the order of one hundred or more times that which is free in solution in the peat water (Gorham, 1956a; Malmer and Sjörs, 1955), and adsorbed calcium, magnesium, potassium, and sodium probably make up a large part of the total sum of these ions in the peat (Malmer and Sjörs, 1955; Gore and Allen, 1956; cf. also Mitchell, 1954). This is likely to be of the utmost significance in plant nutrition. Roots may draw directly upon the cation swarms concentrated around the colloidal soil particles, without the mediation of the extremely dilute soil solution, through a mechanism known as "contact exchange" (Jenny, 1951). By this process (illustrated in Fig. 1) the root surfaces, saturated by hydrogen ions and in close juxtaposition with soil particles, give up these ions in return for potassium, calcium, and other nutrient cations adsorbed on the particle surfaces. In this connection, plants in ombrogenous bogs must have especially difficult nutritional problems, in so far as the concentration of nutrients in the water is extremely low, and the peat colloids are already highly saturated by hydrogen ions, which are the plants' means of exchange. Puustjärvi (1955) has recently shown a distinct correlation between the percentage base saturation of a number of bog mosses and the quality of the peat upon which they grow. It may also be noted that not only the absolute levels, but also the relative proportions of nutrients, are capable of affecting plant uptake and growth; and this is true of both adsorbed and freely dissolved ions (Olsen, 1950; Vlamis, 1949; Heslep, 1951).

Other elements are also distributed differently in ombrogenous sites and those fed by some proportion of mineral soil water (cf. Kivinen, 1938; Waksman, 1942). Of these, phosphorus is perhaps the most important. This element, very scarce in rain, is probably extremely deficient in ombrogenous raised and blanket bogs, and perhaps too in many fens. Phosphorus fertilization has a marked effect upon plant growth in such habitats (Malmström, 1952; Tamm, 1951, 1954). The percentage of nitrogen in the organic matter of ombrogenous peats is likewise low, reflecting the peculiarly low nitrogen content characteristic of the bog moss *Sphagnum* (with its abundance of dead cell walls), whether growing under the influence of mineral soil water or not (Gorham, 1953b). Available nitrogen is probably also deficient in wholly rain-fed bogs (Tamm, 1951), and certainly the concentrations of nitrates are vanishingly small (Pearsall, 1938; Gorham, 1956b). The low nitrogen percentages may well be at least partly responsible for the slow rate of decay of *Sphagnum* peats. However, mineral fertilization may affect nitrogen turnover in peat quite appreciably (Tamm, 1951, 1954).

Iron and manganese frequently tend to accumulate in peaty fen soils flushed by mineral soil water, and in their plants, since the depletion of oxygen in many waterlogged soils allows a high degree of solution of these elements from the soil (Pearsall and Mortimer, 1939; Puustjärvi, 1952; Rankama and Sahama, 1950; Mayer and Gorham, 1951; Malmer and Sjörs, 1955; Gorham and Gorham, 1955; Carter, no date). Silica is also often much more abundant in peats fed by mineral soil water, and dissolved silica may become quite high in alkaline sites. On the other hand, dissolved silica is very low in ombrogenous bog waters (Gorham, 1956b), and this may perhaps be responsible for their poverty in species of diatom algae, which usually possess thick silicious shells or frustules. The silica content of cyperaceous plants tends to increase with site *p*H (Malmer and Sjörs, 1955). Of the trace elements in peat, some evidence from Sweden suggests that boron may be deficient for some plants in ombrogenous areas (Romell, in Malmström, 1952).

From the rather scanty data at present available (Mattson and Karlsson, 1944; Mattson, Sandberg, and Terning, 1944; Gorham, 1953b; Malmer and

Sjörs, 1955), it appears that the chemical composition of plants growing on ombrogenous peats also differs in important respects from that of plants drawing upon water which has percolated through mineral soil. As might be expected, the latter tend to be richer in total mineral material, calcium, silica, and nitrogen. However, Malmer and Sjörs (1955) have reported little difference in the percentage phosphorus of individual species compared on the two kinds of site. Perhaps an increase in growth, rather than a rise in nutrient percentage within the plant, might be expected in response to an increase of what is most likely the chief chemical factor limiting plant growth in ombrogenous habitats. In this connection, there is some tentative evidence to support the general opinion that sites with a more plentiful nutrient supply can produce standing crops distinctly greater than those on sites fed largely by atmospheric precipitation (Newbould and Gorham, 1956; Pearsall and Gorham, 1956; Gorham and Pearsall, 1956b; cf. also Tamm, 1954). It is certainly clear that individuals of many species characteristic of raised and blanket bogs grow there, and compete successfully, at starvation level (Tamm, 1954; Malmer and Sjörs, 1955; Newbould and Gorham, 1956). If protected from excessive competition in richer sites, or if fertilized with the deficient nutrients, they frequently grow much more luxuriantly than in their normal habitats, where their success is probably due to a capacity for withstanding conditions of extreme nutrient scarcity.

It must be borne in mind that the factors limiting plant growth and production on peat may not be the same as those governing the floristic balance in fens and bogs. It might well be, as Malmer and Sjörs (1955) have pointed out, that acidity or ionic balance is more important in differentiating bog and fen communities than available phosphorus, which may be the major chemical factor controlling production.

ENVIRONMENTAL MODIFICATIONS OF THE COURSE OF PEAT ACCUMULATION

While the foregoing picture of bog development, and of the chemical changes consequent upon the cessation of mineral soil-water supply, applies in general to many areas in northern Britain and elsewhere, the way in which peat accumulates varies almost infinitely in response to different combinations of environmental factors. Perhaps the simplest method of demonstrating the effects of environmental variations is to select a series of special cases where the influence of one major factor is of paramount importance, and hence easily perceived. However, it will also be necessary in many instances to point out the effects of factor interaction. Since climate sets the broad limits within which peat formation takes place, it may be considered first.

The Climatic Factor

The chief requisite for bog development is of course abundant moisture. In hot, dry lands peat cannot pile up, and even in the moist tropics or subtropics it does not do so except in alpine regions, or in situations of extremely bad drainage such as obtain, for example, in many parts of Uganda, and, in the New World, in Florida. However, in cool, wet climates, such as that of western Ireland, peat may blanket even the hills and mountains, and cover strongly calcareous soils (Osvald, 1949; Webb, 1947). Thus extremely high atmospheric precipitation, coupled with cool, even temperatures, may allow peat accumulation in sites where, under less wet conditions, the topographic and geological factors would militate strongly against it.

Perhaps the clearest examples of climatic control of bog development have been provided by the Swedish scientist Granlund (1932), who has shown that raised bogs are absent from those parts of southern Sweden with less than about forty-five centimeters of rain per year, while above about sixty centimeters they account for over half the total area of peat land. Above one hundred centimeters of rain, the relative importance of convexly domed, raised bogs tends to decline, owing to a marked increase in the area of ombrogenous blanket bogs, which because of the extreme humidity are able to extend over gently sloping ground.

In a special investigation within the provinces Småland and Svealand, Granlund was able to demonstrate a distinct correlation—for bogs of a similar size—between bog convexity and annual rainfall. For example, bogs of five hundred meters diameter can grow to a maximum of 0.5 meters in height above the surrounding ground, with fifty centimeters of rain. With sixty centimeters, they can grow up to 1.7 meters, with eighty centimeters to 2.6 meters, and with one hundred centimeters of rain the bogs may become raised to the extent of 3.4 meters. For bogs of two hundred meters diameter, the corresponding heights are about 0.4, 1.1, 1.7, and 2.1 meters. Thus under eighty centimeters of rain, a bog two hundred meters in diam-

eter may grow as high as one of five hundred meters diameter receiving only sixty centimeters of rain.

It also appears from Granlund's studies that in the drier climate of eastern Sweden the raised bogs are often covered by pinewood, whereas in the extreme southwest, where rainfall is highest, very few pine bogs are found. With reference to a wider area, it may be pointed out that wooded raised bogs are the rule in Poland (Kulczynski, 1949), with a distinctly continental climate, but are absent (except in artificially drained sites) in the present wet oceanic climate of the British Isles. They were, however, common in earlier phases of dry climate.

A feature of interest here is that bog growth appears to have been affected greatly by climatic fluctuations in the past. Under dry conditions, heathy species, cotton grass, and pine trees tend to be prevalent on ombrogenous bog surfaces in Britain, and the *Sphagnum* remains decay more readily; whereas in a very wet climate they are preserved almost unchanged, and the other species are far less abundant on the bogs. Thus the peat laid down at any time reflects to some extent the climatic conditions of the period, and the presence in most European bogs of horizons of highly decomposed *Sphagnum* peat rich in heath roots and twigs, cotton grass tussock bases, and sometimes pine stumps, suggests marked climatic shifts during the post-glacial era.

According to Granlund, a *Sphagnum* bog could be expected to grow rapidly to its rainfall-conditioned maximum height, whereupon its surface would become better drained, and overspread with species typical of drier conditions; in addition a more highly decayed peat would be formed. An increase in rainfall would then accelerate *Sphagnum* growth again, until the new maximum height was attained. Presumably if rainfall then decreased by a great deal, the convexity of the bog would be too great for it to remain waterlogged at the surface, in which case the uppermost peat might be expected to dry out, decay, and perhaps eventually erode away. However, Granlund's data are interpreted to indicate a generally rising precipitation during the past five thousand years or so, without any marked reversion to a dry climate. A possible alternative interpretation has been suggested by Sjörs (in litt.). If during dry periods a highly decayed peat is formed it will be relatively impermeable (cf. Malmström, 1923), so that an increase in climatic humidity to the previous level might well bring about sufficient waterlogging above the newly formed impervious layer to initiate further bog growth above the previous maximum height. In this way there is less need to assume a progressive rise in climatic humidity during successive wet periods. Certain objections to the simplicity of Granlund's hypothesis have also been raised by Godwin (1946), who prefers to view the activity of a raised bog as controlled by cyclic climatic changes irrespective of its height or convexity. Such an interpretation has many merits, and does not exclude the possibility that climatic shifts will have their greatest effect upon bogs which have attained the greatest height. An interesting point about the main "recurrence surface" (as the boundary between highly decayed and well-preserved *Sphagnum* peat—which marks the climatic shifts—is called) is that it often seems to have arisen from a catastrophic flooding of the existing rather dry bog surfaces, as witnessed by the abundance of the more aquatic bog plants at the immediate junction (Clapham and Godwin, 1949). In this connection, Conway (1948) has suggested the possibility that short-term climatic cycles may have a marked effect upon the balance between hummocks and hollows on the bog surface, and also that gradual long-term shifts may sometimes initiate rather sudden "threshold" responses by the vegetation, with rapid changes once the boundary of climatic tolerance between two communities has been crossed. The aforementioned phenomenon of "biological inertia" may perhaps be involved.

An interesting suggestion concerning the effects of climatic fluctuation has been made by Mölder and Salmi (1955), in their discussion of the peats of the Vaasa district in Finland. There the 50-meter contour divides poorly humified coastal peats from mostly well-decayed upland peats. This contour marks the late-Littorina Period sea level, and during this era conditions seem (from pollen analyses) to have been wet and warm. Thus many bogs began to form at that time on the freshly exposed land surface, but peats tended to decompose readily. After the Littorina Period the climate became cooler, and bogs which originated after that time (chiefly on land below 50 meters) accumulated relatively well-preserved peats. The above situation illustrates most strikingly the interaction of moisture, temperature, and relief as factors conditioning peat accumulation.

The general role of temperature in determining the course of bog development can be seen from the prevalence of peat lands at high latitudes. The kind of bog formed is also governed partly by

temperature (Sjörs, 1950b), for as one progresses northward in Sweden the lessening of evaporation acts to some extent in the same way as an increase in precipitation, and favors the development of various types of blanket peat on sloping ground. However, Sjörs (in litt.) suggests that, given two identical landscapes of equal climatic humidity, some areas which would remain as flushed mineral soils in western Europe would be covered by sloping fens in the north, while certain of the flat mineral soils developed as podzols in the north would correspond in situation to some of the blanket bog formations in the west. In the valleys of the north, "ribbed mires" are often formed in which hummock banks of bog vegetation, raised by frost action at right angles to the line of water flow, separate wet fen areas.

In the extreme north of Scandinavia, under a severely cold winter climate with strong winds and little snow, and with the subsoil permanently frozen, a peculiar form of peat deposit called "pals bog" occurs (Lundqvist, 1943). The "palses" are huge peat hillocks pressed upward from the surrounding fen, and frozen inside. They become very dry at times in summer, and carry a bog vegetation rich in lichens.

Kellogg and Nygard (1951) have pointed out that in Alaska the permanently frozen subsoil leads to waterlogging and peat formation even on fairly steep slopes. However, in eastern North America Potzger and Courtemanche (1955) found only very shallow peats of no more than 60 centimeters depth within the permafrost zone. The depths of peat encountered by these workers in going from the St. Lawrence River valley to Payne Bay in northern Ungava decreased steadily northward. In the St. Lawrence valley peat deposits may exceed thicknesses of 10 meters, at Mont Tremblant (46° N) bogs may reach about 8 meters depth, beyond Clova (48° N) about 5 meters, at Rupert River (51° N) about 3 meters, and at 55° N (in the forest-tundra transition belt) about 2 meters). In the tundra proper no typical *Sphagnum* bogs were observed, and peat depth seldom exceeded 60 centimeters, as noted above.

Another climatic factor of some importance is the supply of nutrients from the atmosphere, via sea spray, rain, dust, industrial pollution, etc. Since ombrogenous bogs derive almost all their nutrient salts in this way, a difference in the amount supplied in various areas may be of great significance. While relatively few data are available at present, in Sweden there appears to be a marked southwesterly increase in the amounts of sodium, chloride, potassium, ammonia, and nitrate supplied to the soil by rainfall (Emmanuelsson, Eriksson, and Egner, 1954; Eriksson, 1955), with which may be associated certain floristic differences (Du Rietz, 1949). For example, sweet gale (*Myrica gale*), the cotton grass *Eriophorum angustifolium*, the bog moss *Sphagnum papillosum*, the blue-green alga *Chroococcus turgidus*, and the diatom *Frustulia rhomboides*, all present in fens receiving mineral soil-water in southern Sweden, are absent from raised bogs in the east but are sometimes or often present in the west. They are also all present on ombrogenous bogs in Britain, with a host of other plants commonly absent from ombrogenous sites in Sweden, including the bog mosses *Sphagnum recurvum*, *S. pulchrum*, and *S. subsecundum*, the bog asphodel *Narthecium ossifragum*, the purple moor grass *Molinia caerulea*, the algae *Tetmemorus grandis*, *T. laevis*, *Netrium digitus*, and many others. Moreover, in western Ireland the ombrogenous blanket bogs are generally dominated by the black bog rush *Schoenus nigricans* and the purple moor grass *Molinia*, instead of *Sphagnum*; and they possess many other species regarded elsewhere as more typical of fens supplied with mineral soil water. Indeed, on the continent *Schoenus* is regarded as a species of calcareous habitats. An explanation has been offered in terms of increased sea spray (Tansley, 1939; Osvald, 1949; cf. Gorham, 1953c), but seems unlikely to be valid in view of recent investigations (Gorham, 1956b; Pearsall, 1956). These have shown that in northern England and Scotland no such important floristic differences are apparent in bogs situated very near the sea shore, and receiving exceptional quantities of sea spray (as shown by the very high levels of sodium and magnesium chloride in their waters).

Previous studies (Pearsall and Lind, 1941; Gorham, 1953c) have been taken to indicate a much lower acidity in the peats of these western Irish *Schoenus* bogs than in normal *Sphagnum*-dominated ombrogenous bogs. However, recent investigations (Gorham and Sjörs, unpub.) of undoubtedly ombrogenous bogs in Ireland, with and without *Schoenus*, and in Great Britain, have failed to show any significant differences in the chemical composition of water samples from bog pools where *Schoenus* is present and where it is absent. Moreover, the western Irish bogs in general show little chemical difference from normal inland

British and Irish bogs except as regards sea spray effects.

Another point emerging from chemical analyses of rainfall may be of interest (Gorham, 1955a). It is likely that industrial contamination of the atmosphere has led to a marked increase of sulfuric acid and ammonia in rainfall, and also perhaps of potassium and calcium. While the biological consequences are not easy to establish, they may well have been appreciable, and some of the deleterious changes in moorland floras ascribed to drainage, burning, and grazing have perhaps been assisted by increasing acidity (or other changes) in the rain. In contrast, the added nitrogen and mineral supply may have been beneficial. In this connection, Swedish soil scientists (Mattson and Koutler-Andersson, 1954) have suggested the possibility of a phase of rapid bog growth in recent centuries, dependent upon the increased atmospheric supply of minerals from wind erosion of cultivated soils, and of nitrogen from fossil fuels. It may be pointed out that atmospheric ammonia may be absorbed by acid humus directly from the gaseous state, without the necessity for washing out by rain, and ammonia is an important component of atmospheric pollution.

A last climatic factor to be mentioned is wind. Both the direction and strength of the wind influence atmospheric precipitation of various elements in large measure (Gorham, in prep.). Wind is also an active agent of peat erosion. The Swedish ecologist Osvald, who has had much experience of British peat lands also, states (Osvald, 1949) that many cases of blanket bog retrogression are due primarily to wind erosion. After high winds have scooped hollows out of the peat, water erosion can connect these into a system of channels, whose orientation depends upon the prevailing direction of the eroding winds, and upon the slope. Osvald also believes that freezing temperatures are necessary for serious wind erosion in Britain, although on the European continent the longer periods of summer drought may provide similarly suitable conditions.

A minor effect of wind, upon the orientation of hummocks and the distribution of plants on them, has also been noted by Osvald in Britain. Under severe wind stress, normal growth often takes place only to leeward, being largely inhibited on the eroded and over-steepened windward side. In less extreme cases, the plants to windward and leeward may be quite different. For instance, in the Wicklow Mountains of Ireland, the mosses *Rhacomitrium lanuginosum* and *Leucobryum glaucum*—commonly dominant on high hummocks—in general seem to favor the windward and leeward faces respectively. A most extreme case of this phenomenon has recently been recorded by Roivainen (1954, pp. 149–150) from Tierra del Fuego, where he describes a whole bog ribbed by banks of *Sphagnum magellanicum* at right angles to the prevailing wind.

A rather similar development is reported from Australian bogs by Millington (1954). There hummocks apparently form in the shelter of shrubs, such as *Epacris brevifolia* and *Callistemon sieberi*. Under the former, as the hummock grows in height, wind tends to erode it on the westerly face, so that the hummock gradually shifts to leeward, where *Sphagnum* growth remains active. However, there is evidence that once the hummocks have been moved away from the shade of the shrub, they suffer from exposure, and may stop growing or even decay, unless new shrubs become established. In the denser shade of *Callistemon*, the moss grows best toward the edge of the canopy, so that the bush comes to stand in a "saucer" of *Sphagnum*. Under continuous shrub cover, on the other hand, hummocks completely fail to develop, and the bog surface is smooth and even.

The Topographic Factor

The main ecological function of land form lies in determining local moisture conditions, as against the general pattern controlled by climate; but the nature of the relief also has an important influence upon the flow of nutrients leached from the soil by rain. W. H. Pearsall (1950) has dealt at length with the topographic factor in relation to British moorlands and bogs, and his description of the influence of slope upon vegetational distribution in the northwestern Scottish Highlands serves as an excellent illustration of its importance under very wet climates.

The major plant communities of the area are birchwood and bog, with the woodlands commonly restricted to the well-drained and richer soils of unstable or recently stabilized slopes, and the bog lands of deep peat occupying the gentler slopes and flat ground of both the plateaus and the valley bottoms. Of the various kinds of bog vegetation, deer grass (*Trichophorum*) communities with purple moor grass (*Molinia*), bog moss (*Sphagnum*), and heather (*Calluna*) usually cover the deeper peats on the flatter parts of the pleateaus. Heather moor may dominate the better-drained upland

situations, often at the steepened transition zone between the deer-grass bog and the birchwoods, although *Molinia–Myrica* communities are prevalent wherever a peaty flush from the bog above makes the soil sufficiently damp. Below the birch woods, as the slope becomes gentler again and percolating waters seep out at the soil surface, *Molinia–Myrica* areas are generally found—sometimes with remains of alder and birch from an earlier damp woodland phase. Alder still persists in some of the more silted zones along streams in the valley bottoms, but on the flat and poorly drained ground farther away from the streams, deer grass and bog moss may combine with the purple moor grass to form deep peats resembling those of the uplands in their ombrogenous character.

In the wettest parts of Britain, deep blanket peats cover quite steep slopes, up to one and one-half meters of peat being sometimes recorded on slopes of twenty degrees, or about one in three. In such situations, as the bog grows it must either develop its own internal drainage system, or eventually become so big that the accumulation of water during heavy rains may exceed the holding capacity of the peat, and lead to a flow of the whole mass downslope (Früh, 1897; Granlund, 1932; Osvald, 1949). Slight changes of slope may also be of decisive importance for the stability of blanket peat deposits. Where such a bog, during its development, overgrows the steeper margins of a plateau or hanging valley, exceptional rainy periods may likewise cause the bog to flow at that point, and huge blocks of peat to slide down from above.

A somewhat similar overgrowth phenomenon has been observed on a much smaller scale in some Australian swamps (Millington, 1954). These have grown gradually upslope in the granite gullies of the Snowy Range, owing to restriction of seepage and backing up of the water table by peat accumulation around the original spring. With the advent of heavy rains, a head of seepage may build up in excess of the peat's ability to contain it, and water-inflated "blisters"—six to nine meters in diameter and up to sixty centimeters high—form toward the lower end of the swamp, and eventually burst.

It has been suggested by Conway (1954) that climate and topography have combined on a more general scale in Great Britain, to bring about a great deal of peat erosion in the Pennine uplands during fairly recent times, widely assisted by human agencies. At altitudes over 370 meters, the wet climate initiated at the Boreal Atlantic Transition (about 6,000 B.C.) gradually resulted in extensive peat formation in favorable topographical situations. However, the excessive wetness of the last two millennia appears to have brought about extremely rapid accumulation of loose, undecayed *Sphagnum* peat in the uplands, where rainfall is heaviest. This eventually led to mechanical instability and widespread peat erosion above about 450 meters. The influence of man (forest clearance, grazing, and burning) appears to have accentuated erosive activity during the last thousand years, and to have prevented the normal healing process of *Sphagnum* regeneration which tends to counterbalance erosion.

In the more continental climate of Poland, erosive forces are naturally less catastrophic, but Tolpa (1947) has described a case where, in an upland bog of a rather more atlantic type than usual, erosion has led to the formation of large "peat lakes" on top of an extensive convex deposit of *Sphagnum* peat.

Concerning the distribution of Swedish peat types in relation to relief, Sjörs (1948) has noted that in northern Sweden ombrogenous bogs tend to occur on the more permeable glacial sands and gravels of the valleys, while the less porous till of the hills and plateaus favors fens influenced by mineral soil water.

In the distinctly continental climate of Poland, topography assumes a very important role in determining the course of bog formation, and Kulczynski (1949), in his fascinating treatise on the peat deposits of the Polesie Basin, discusses at great length the complex ways in which relief conditions peat accumulation. An important point about bog development in Polesie, which must be firmly grasped, is that vegetation generally characteristic of truly convex raised bogs elsewhere is found upon peat surfaces which are not apparently raised above ground water level, but which are nonetheless called raised bogs—according to their floristic affinities and type of peat. Only in a few instances, where the peat deposits are over a kilometer in diameter, does a slight surface convexity become discernible, and it is only in these bogs that true "hummock and hollow" regeneration complexes have been recorded.

Kulczynski's main thesis is that the principal division, into "raised" and valley bogs (these latter are all fens in the terminology of Du Rietz, 1949), is dependent upon water flow. Sites receiving a terrestrial inflow of enriched mineral soil-water do

not develop into "raised bogs," but remain as valley bogs, dominated by reed swamp, sedge fen, or carr woodland communities. While in sufficiently oceanic climates the bog moss may invade such areas, and form true raised bogs on top of them, this is not possible in the drier Polish climate, with its well-marked water-balance deficit in summer (evaporation exceeding precipitation). Thus in Polesie the development of vegetation-designated "raised bogs" is restricted to watersheds, where the moisture supply is entirely atmospheric, and therefore deficient in nutrients. An example of the delicacy of vegetational adjustment to the hydrological regime is given in Fig. 2 (drawn after Kulczynski), where a rise in ground water table of one and one-half meters, in a sandy dune ridge spanning three kilometers, is enough to differentiate the wet-hollow communities on the ridge into "raised bog" or transitional "raised bog," in contrast to the typical valley bogs found on the lower ground to either side. Under continental climatic conditions the surfaces of all bogs conform to the ground water table. However, in the Polesie "raised bogs" this ground water table, which may be convex as shown in Fig. 2, merely represents the hydrostatic equilibrium between gravity and soil capillarity, and is regenerated solely by rain falling directly upon the watershed. Only where the percolating surplus moisture, enriched in nutrients, seeps out from the subsoil into the valleys, are the reed swamps, sedge fens, and alder-willow carrs of valley bogs able to develop.

If on such a ridge as that in Fig. 2, the slope is very gentle and the water table sufficiently high, "raised bog" coverage will assume much greater proportions, so that a blanket peat—evening up minor irregularities in the landscape, and somewhat resembling those of oceanic climates—will be formed. However, in this instance it will be more directly limited by the level of the ground water table than is the case with its more westerly homologues.

It should be pointed out that there are occasions on which valley bogs become transformed into "raised bogs." Rather paradoxically, this occurs as a result of the removal of river-water drainage into the valley bog, usually owing to river capture. By this means, terrestrial inflow of mineral soil-water may be diverted, and the site removed from the stream network onto a terrace or water-shed where it receives only rainwater. The diminution of nutrient supply consequent upon the change in water regimen leads to development of pinewood and *Sphagnum* hummocks, and metamorphosis into a typical "raised bog."

Such phenomena may also be observed to cause development of truly raised bogs under wetter conditions. A good example is described by Kulczynski from the Carpathian district of southern Poland, in a damp mountain climate (annual rainfall about eighty centimeters). This bog has, except at the edge, a treeless dome of *Sphagnum* peat ten meters

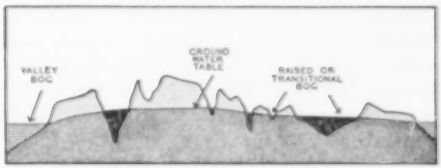

FIG. 2. DIFFERENTIATION OF POLISH BOG TYPES IN RELATION TO TOPOGRAPHY AND HYDROLOGY
(After Kulczynski, 1949). Vertical = 700 × horizontal scale. Explanation in text.

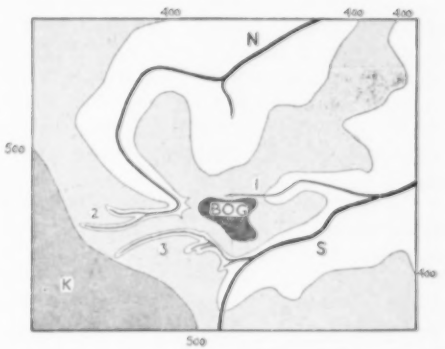

FIG. 3. TRANSFORMATION OF FEN INTO RAISED BOG THROUGH RIVER CAPTURE
(After Kulczynski, 1949, schematized). Explanation in text.

thick, overlying fen peat and lake muds. At the boundary between the fen and the *Sphagnum* peats is a horizon of forest peat. The bog lies, as shown in Fig. 3 (after Kulczynski), in a shallow depression of a gently eastward-sloping terrace, on the water-shed between two large rivers (N and S). It is drained on its north side, by a small stream (1) leading east through a wide depression, into the southern river. The hill (K) to westward is drained by two small streams (2 and 3) coming down in narrow gorges onto the bog terrace, where they diverge sharply north and south to feed the large rivers N and S.

It appears highly probable that in the past streams 2 and 3 flowed through the bog site, which at that time was occupied by fen, into stream 1. (The old fen surface slopes to the east, and not toward the present drainage line along the north side of the bog). Then, as tributaries from the large rivers to north and south cut back into the bog terrace, they captured streams 2 and 3, thus removing from the fen its terrestrial inflow of mineral soil-water, and providing conditions suitable for a forest invasion, and subsequently the development of raised bog *Sphagna*.

In Britain the cutting back of streams may also have marked effects. According to Pearsall (1950), it may frequently be the cause of extensive peat erosion from the upland blanket bogs of the mountain plateaus, along with bog flows, and the overdevelopment of internal drainage channels beneath the peat—which may lead to collapse of the peat above and gully-formation throughout the bog.

Stream silting may also have important consequences for bog development. Pearsall (1918) has ascribed the differentiation of fen meadows laterally from the principal inflow into Esthwaite Water to this factor, with reedgrass communities on the heavily silted stream embankment, and sedge associations on the more peaty soils forming farther away.

The effects of silting upon bog development are extremely well illustrated by Darlington's (1943) extensive investigation of Cranberry Glades, in West Virginia, U.S.A. In this rather southerly location, *Sphagnum* bogs are found chiefly in the mountains, and at Cranberry Glades they are further favored by the presence on Cranberry Mountain of numerous cold springs, which feed the streams running through the peaty flats. However, the pattern of peat accumulation (which exceeds three meters in places) is largely dictated by local relief, controlled in turn by the nature of the underlying rocks.

The peaty area occurs near the source of the Cranberry River, in a wide valley believed to have developed through the damming back of drainage by hard conglomerate rocks downstream, which led to sideward stream-cutting and base-levelling in the softer shales beneath the present Glades. During late glacial times, when the swollen streams were heavily laden with soil eroded from the bare mountain sides, interposition of the level valley floor in the stream courses caused much of the suspended material to sediment there, with the coarser gravelly fractions building up embankments or levees along the stream sides, and the finer clays settling in the ponded hollows forming behind the levees, especially in the angles of stream junctions. In the post-glacial period, plant growth initiated peat accumulation in these poorly drained depressions (which make up the present open "glades"), while levee-building slowed down and gradually ceased—due to lessening water supply, increasing vegetation cover on the mountains, and also to capture of large areas in the Cranberry River drainage basin by the Greenbrier River system, cutting back into the softer rocks of the Cranberry headwaters.

Vegetation distribution followed the drainage pattern, with a bog forest of spruce (*Picea rubens*) on the moderately acid soils (*p*H 4.5) along the margins of the valley, *Alnus incana–Sambucus canadensis* shrub communities on the circumneutral silts (*p*H 6.1) of the stream courses, *Alnus incana–Viburnum cassinoides–Sphagnum palustre* communities on the shallow acid peats (*p*H 4.4) adjoining, and more typical fen and bog associations on the deeper peats of the old ponded depressions. Among these, *Carex rostrata–Sphagnum capillaceum* communities occupy the moderately acid deposits (*p*H 4.4) most subject to flooding by mineral soil water from the streams, with *Sphagnum capillaceum*, *S. palustre*, *Vaccinium oxycoccus*, and *Rhynchospora alba* associating on slightly deeper and considerably more acid peats (*p*H 4.0). The drier and slightly elevated central peats of the glades, which are wholly ombrogenous and very acid (*p*H 3.8), are covered by *Polytrichum* (*strictum*, *ohioense*, and *commune*) and *Cladonia* (*rangiferina* and *tenuis*) communities. *Eriophorum virginicum* grows over the whole of the open glades, and provides a common autumnal aspect for several communities.

Regarding the future of the area, bog forest is now encroaching on all sides, and this sign of increasing drainage is supported by the fact that the Cranberry River has lately cut a new and almost straight course through the glades to replace its old meandering channel. Such rejuvenation is probably consequent upon the river's having finally cut through the hard Princeton conglomerate downstream, into softer Hinton strata. Further and more rapid stream-cutting may be expected to lead eventually to increased peat erosion, and ultimately to colonization of the glades by the normal hardwood forest of the region.

Yet another American instance of levee-forma-

tion leading to peat accumulation, in this case very recently, has been given by Potzger (1934). In the Indiana site he described, a large stream has succeeded in ponding off a small inflow behind its silt embankment, with consequent death of forest trees and development of *Sphagnum* on as much as six feet of peat in the deepest part of the basin.

In Polesie, it has been shown that topography can, through its influence upon nutrient supply (*i.e.* enrichment by terrestrial inflow), determine whether or not "raised bog" development will take place. It may also, through purely hydrodynamic effects, be decisive for the course and extent of peat accumulation by valley bog communities of reed swamp, sedge fen, and carr woodland. Evidently, unless the water table gradually rises, peat deposition by any one of these communities will not go on for long, as the concomitant shallowing of the basin will initiate vegetational succession. However, in certain situations the formation of peat may itself retard water flow, and thus bring about a sufficient rise in the water table to allow local vegetational stability. In this way thick layers of homogeneous reed, sedge, or carr peat sometimes do build up. The topographic conditions requisite for the deposition of deep valley bog peats must now be examined, following the line of Kulczynski's arguments.

It is clear that peat bogs are not found in every river valley, but only in those where the water volume is small in relation to the size of the valley, and insufficient to induce erosion during flood periods. Since reduction in drainage area is commonly the cause of reduced flow, and is itself most frequently brought about by river capture, extensive peat bog development of both the "raised" and valley bog types should be looked for, according to Kulcyznski, in the vicinity of watersheds, where river capture is most frequent. In this connection, Polesie—the largest marshy district in Europe—lies on the main European watershed, between the Baltic and the Black Sea. It has also experienced vast hydrogeological changes in postglacial times, owing to capture of large parts of the original drainage basin (of the proto-Pina River) by the rivers Bug and Niemen, and in southern Polesie to extensive shortening of the river systems, which now run mainly south to north instead of southwest to northeast.

Where the general land form is thus favorable to bog development, subsidiary factors such as the shape and size of the local drainage basins may, by influencing water inflow and retention, determine the course such development will take. In all but very small drainage basins, wherever the relief promotes water retention, the vegetable debris will remain water-soaked for long periods, and well preserved. They will therefore be light in weight and, floating to the surface at high water, will retard water flow even more. In Polesie, slow flow appears to produce sedge fens with well-developed moss layers. On the other hand, where water retention is not so great, the vegetable remains will be exposed more often to the air, and hence be more decayed, heavier, and more liable to sink. The influx of large amounts of relatively heavy mineral soil materials and slime from outside the bog will add to the sinking tendency. Such heavy slimy peat offers little resistance to a rather strong water flow, which through its erosive power is liable to become distinctly channelled. In such sites reed swamp, devoid of associated moss species, is commonly the dominant plant community.

In valley bogs with very small drainage areas, the precipitation deficit during summer in Polesie is of course an important factor, inhibiting to some degree the formation of mossy sedge meadow even in places with marked powers of water retention.

The dynamics of land form alter bog development in other ways than by river capture. For example, tectonic upheaval may well explain stratigraphical anomalies due to erosion in the great Degerö Stormyr bog complex in northern Sweden (Malmström, 1923; Kulcyznski, 1949). And changes in the relative levels of land and sea have had a profound influence upon vegetation succession and peat accumulation in the fens of East Anglia (Godwin and Clifford, 1938) and of the Norfolk Broads district (Lambert, 1953).

The gradual emergence of the Fennoscandian land mass from the sea during postglacial times has also had a strong influence upon the pattern of bog distribution. A recent account of peat lands in the Vaasa district of west central Finland provides evidence on this point (Mölder and Salmi, 1955). In this region, where peat formation takes place not only in water-filled basins, but also on normal forest land, the uplands exhibit a much greater peat coverage than the more recently exposed coastal areas, largely because of their greater age. In this connection, along the coast many bogs are entirely covered by one type of vegetation, while in the uplands they have spread and merged extensively so that bog complexes with a number of plant communities are more often encountered.

Peat deposits are most abundant on the water-

sheds where the big rivers rise, and a greater proportion of open *Sphagnum* bogs is found there than elsewhere. However, in the neighborhood of the two main river systems the increased efficiency of drainage has restricted peat accumulation, although the rivers flow through very boggy districts. It may be noted that the land uplift has in many cases affected the drainage pattern strongly, so that lakes have transferred their outflows from north to south or southeast. This has resulted in many southern shores becoming boggy, while peat is frequently absent from the northern edges.

As might be expected, bog types show a close relation to altitude in this district. The more eutrophic reed, sedge, and grass bogs occur chiefly on the coast, where the area of peat land is insignificant. These are rather wet bogs in general, especially the reedy ones which are as a rule only a meter or so above sea level. The grass and sedge bogs, which succeed the reedy types in the 1–5 meter zone, are drier and more mossy. Pine bogs account for much of the bog area more than 5 meters above sea level, where drainage is better. Pine bogs with *Ledum palustre* are common in the 5–10 meter zone, but other types are most frequent between 10 and 18 meters. Above 18 meters raised bogs appear, and *Sphagnum* becomes more important.

It is of course true that the above differences are partly developmental, for the upland bogs exhibit in their profiles reed, sedge, and grass typical of earlier stages in the plant succession. However, the uplift does exert some influence upon drainage, and it is probably true to say that unless it were taking place the older bogs might have undergone a different and wetter type of development.

The importance of relief in relation to nutrient flow may be noted in connection with the chemical differences between ombrogenous and other types of bogs. As a further example of its influence, some recent data from Cranesmoor—a valley bog in southern England—may be of interest (Newbould and Gorham, 1956). On this area of deep peat, two diffuse inflows bearing chiefly *Schoenus nigricans–Moliniacaerula–Myrica gale* communities enclose a slightly raised area, still receiving some inflow off the mineral soil but dominated by *Sphagnum papillosum* and *Rhynchospora alba*. The adsorptive capacity of the peat in the vicinity of the inflows is generally slightly more than half saturated by metallic cations, while in the less flushed central *Sphagnum* patch hydrogen ions predominate by a small margin. Similarly, the lines of inflow are characterized by waters rather less acid and somewhat richer in mineral salts than those of the *Sphagnum* area. However, it may be doubted whether these differences (water *p*H 5.1 as against 4.8, a twenty per cent difference in specific conductivity of the water, and 58 as against 45 per cent metal cation saturation of the peat) are of the first importance to the vegetation. What may be of greater significance is the fact that nutrient supply per unit time must be much greater in the more flushed lines of inflow. In this connection, the total dry weight of green plant material per unit area has been found to be about two and one-half times as high in the *Schoenus–Molinia–Myrica* communities as in the *Sphagnum–Rhynchospora* enclosure. In addition, the former vegetation has about twice the percentage of mineral ash, and one and one-quarter times the percentage of calcium in the *Sphagnum*-dominated vegetation, so that the total uptake per unit area is far higher in the sites receiving more inflow. These facts tend to support the view that there is a much greater absolute nutrient supply along the lines of inflow than the differences in acidity and base status would suggest. The constant water movement also ensures that diffusion pockets will not develop around plant roots and thereby retard the rate of ion uptake (Olsen, 1950). It may further be remarked that individual tillers of several species are heavier in the more flushed areas than in the central *Sphagnum* island.

To conclude this discussion of the topographical factor, a somewhat paradoxical relation between peat formation and relief—observed at Carrowkeel in Ireland by Webb (1947)—may be mentioned. In this district, the highly humid climate permits peat accumulation in some places even on a rather dry limestone substratum, and in the transition between grassland and moorland, peat is found to accumulate chiefly on knolls or other better-drained situations. This phenomenon may be explained by assuming that the climate is sufficiently wet to allow peat formation even on the best drained soils, and that its development is restricted to them, owing to the absence there of calcareous flush waters inimical to the growth of moorland species and favorable to peat decay.

The Geological Factor

Geology conditions bog development both physically, through its effects upon the permeability and erodability of the soil, and hence upon water relations, and chemically, by its effects upon nutrient supply.

With regard to the physical factor, the Cranberry Glades bogs discussed earlier (Darlington, 1943) provide a striking illustration of its influence. Rigg and Strausbaugh (1949) have also pointed out that in these cool, moist mountain situations in West Virginia the hard Pocono sandstones favor *Sphagnum* bog formation, in two ways. First, depressions in such rocks are slow to drain, owing to the difficulty of stream cutting; and second, the sandstones may dam up drainage of streams flowing through softer rocks above (e.g. Greenbrier limestone), and thus create waterlogged flats suitable for *Sphagnum* growth. (A third possibility is that the slow-weathering sandstones may be very poor sources of nutrients, and thus favor peat accumulation in this way too).

A few additional examples of physical controlling factors may now be quoted briefly. Pearsall (1950) has suggested that in northern Britain the frequent formation of iron pans in the more sandy and porous substrata may lead to waterlogging, and finally to peat accumulation. By way of contrast, in the Snowy Range of Australia it appears (Millington, 1954) that granite soils are more favorable to the building up of thick peats than basaltic types, chiefly because of the greater permeability and depth of the former, which favors the accumulation of large subsoil water reserves.

The development of bogs in karst limestone sinkholes, where puzzling alternations of peat types may occur, provides a further illustration of the action of the geological factor, partly physical and partly chemical. Kulczynski (1949) reasonably ascribes such phenomena to subsurface slumping of the limestone brought about by the formation of underground solution channels. In this way a peat surface which had built up to slightly above water level, and had thus become more acid and less well supplied with bases, as well as changed floristically, might be reflooded with alkaline water from the solution hollow, and revert to its original chemical and floristic state.

The purely chemical aspects of the geological factor are also of much importance in differentiating peats and their plant communities. For instance, the floristic richness of fens in limestone country has long been recognized, and has been discussed in detail for Swedish habitats by Du Rietz (1949) and Witting (1947, 1948, 1949). The latter author has carried out extensive cation analyses of fen waters in numerous sites, clearly showing correlations between plant distribution and their base status and acidity, which in many cases depend upon local geology (cf. also Gorham 1955b).

In the East Anglian fens the local importance of geology, through its influence on the alkalinity of the surface drainage waters, has been most evident in the investigations of Godwin and Clifford (1938). In the Woodwalton basin, with lime-poor drift and no large rivers, raised bogs developed extensively in postglacial times; whereas in the other parts of East Anglia, fed by large rivers off the chalk, such communities occurred only marginally, or during dry climatic phases when the peat surfaces were less likely to be flooded by lime-rich waters.

The interrelation of topographic, climatic, and geologic factors has also been outlined for the Somerset levels in Britain (Clapham and Godwin, 1949). There, during two periods of suddenly increased rainfall, the raised bogs of the poorly drained coastal clay plain were widely flooded by calcareous drainage from the surrounding limestone uplands, and became colonized by the sawsedge *Cladium mariscus*. Only a few bogs in exceptionally elevated or otherwise protected situations escaped this influx of calcareous water, and even they reflected the change in humidity by becoming covered with more aquatic—though still acidic—plant communities. A possible alternative explanation of the later flooded horizons is that they developed in response to drainage changes brought about by marine transgression (Godwin, 1949).

Regarding the correlation between peat type and underlying rock, Tamm (1950) has pointed out that in Sweden the local geology may modify the general climatic control of peat quality, as judged by its suitability for forest growth after drainage. Where limestone or clay schists are found, peats may be amenable to forestry operations even where the humidity is rather high. However, on quartzites, sandstones, and porphyry, forestry may be impracticable even although the climate is relatively dry. In Finland, Mölder and Salmi (1955) record that *Carex*-dominated peats are chiefly concentrated upon basic bedrocks or those with minerals rich in mica. Biotite gneisses favor woody peat types as well. It is also reported that the usual oligotrophic pine bogs may be replaced by eutrophic types in certain limestone areas.

A British example of the dependence of peat type upon underlying rocks has recently been furnished by Moore (1954). It is claimed that the boundary between *Trichophorum caespitosum* and

Eriophorum vaginatum bogs in the Wicklow Mountains of Ireland depends not so much upon altitude—which was formerly thought to be the case—as upon the transition from granitic substrata (with *Trichophorum*) to shales and schists (with *Eriophorum*), the vegetation following almost exactly the line of contact between the rock strata. According to Sjörs (in litt.), no similar relationship would be expected in Sweden, however.

A new field of peat chemistry which is only now beginning to be studied is that concerned with the so-called trace elements, such as zinc, copper, lead, cobalt, nickel, chromium, arsenic, molybdenum, boron, etc., whose distribution is probably related in large measure to local geology. Preliminary studies have shown great variability in the contents of numerous trace elements in peats from different Scottish bogs, and their distribution within the peat profile also varies markedly (Mitchell, 1954). These elements seem to be present mostly in forms of low solubility, and their biological significance is practically unknown. Salmi (1950, 1955) has demonstrated that in Finland certain trace elements may be concentrated in peats lying near ore or sulfide-bearing rocks.

As a last illustration of the role of chemical factors, the case of the "dead" swamps of southeast Uganda may be described (Chenery, 1952, 1954). In certain parts of the Kigezi district, where Precambrian schists and phyllites are found, and where salt licks of sodium sulfate occur in the hills, peats covered by dense papyrus swamps may cease, upon drainage, to support any higher plant life at all. The explanation given is that sodium sulfate is formed in the hills by oxidation of pyrites and reaction with sodium-rich minerals, and washes into the edges of the swamps. There sulfur precipitates through bacterial reduction as ferrous sulfide. However, upon drainage and oxidation large amounts of sulfuric acid and ferric hydroxide are formed, the *p*H drops below 3, and toxic amounts of heavy metals are dissolved from the mineral fractions of the peaty soils. Reflooding appears to bring about amelioration of the soil conditions and restoration of the papyrus cover.

Similar chemical conditions may be found in certain lacustrine deposits in Scandinavia, some of them rather organic, which have become partially drained through coastal uplift (Wiklander et al., 1949, 1950). Later and more extensive drainage by human agencies has produced very high acidities, in the same manner as in Uganda.

The Biotic Factor

In considering the biotic control of peat development, the well-known effects of human cultural operations (see for example the recent International Peat Symposium held under the auspices of the Bord na Mona, Dublin, 1954) spring first to mind, but need not be examined in detail here. The importance of atmospheric pollution has already been mentioned, and Lambert's (1953) studies on the origin of the Norfolk Broads provide an extreme example of the influence of peat-digging in the past. Among animals other than man, the beaver is probably one of the most influential. In many parts of North America the normal drainage patterns set by topography have been drastically altered by damming, and the distribution of peat-forming plant communities has been correspondingly modified. A noteworthy example of invertebrate animal influence has recently been provided by Hedberg (1954) from tropical East Africa, where tussocky *Carex runssorensis* bogs with interstitial *Sphagnum* carpets are found in certain alpine situations. In this part of the world, it appears that there are species of earthworms which eat *Sphagnum*, thus transforming it into a muddy or crumbly substance very unlike the normal *Sphagnum* peat of the north temperate zone.

There is another and equally important aspect of the biotic factor which deserves recognition, namely, the influence of widely different floristic and vegetation types. For instance, bog development in the Snowy Range of Australia (Millington, 1954), in Uganda (Lind, 1954), and in Tierra del Fuego (Roivainen, 1954) is very different from that of the north temperate zone, in so far as the major peat-forming species are often very different. There appears to be only one species of the bog moss *Sphagnum* in the above-mentioned Australian bogs, and as far as one can gather, the number of species in East Africa and Tierra del Fuego is rather small compared to the wide variety in the bogs of Europe and North America. Even as between northwestern Europe and northeastern America, marked floristic differences are observed, although the major genera of higher plants, and even the species of *Sphagna*, are often common to both (cf. Nichols, 1918; Tansley, 1939). And differences within the European continent, and even inside the British Isles, have been remarked on earlier in the discussion of ombrogenous bog vegetation.

Nevertheless, in spite of such wide floristic di-

vergence, it is indeed remarkable how similar the problems of bog development are in all these areas. In the opinion of the present author, a bog ecologist would probably find it much easier to adjust his preconceptions to work in another of these regions than would his colleagues concerned with forests or grasslands and their soils.

Although it has been little examined, a minor question of some interest arises with regard to subspecific entities within the floras of peat lands. As an example, the case of *Eriophorum vaginatum* might provide a useful subject for such an investigation. This plant commonly occurs on bog hummocks in Britain, and particularly on drained bogs. Moreover, its shoot bases are also very abundant in a distinct layer at the base of the *Sphagnum* peat in certain bog profiles (Rankin, in Tansley, 1911; and personal observation). The natural inference might well be that such a layer represents a phase of surface desiccation, probably climatic in origin. However, in eastern Sweden this species may be more characteristic of hollows, and reach its maximum abundance and vigor in the wet marginal fen (lagg) adjoining most raised bogs, and thus be typical of the stage immediately preceding raised bog development (Du Rietz, 1950; Gorham, 1950). The question might then be posed as to whether the *Eriophorum* horizon deep in the Lake District bog profiles may represent a normal transition phase of development, as in eastern Sweden, or rather a phase of drier surface conditions similar to those of present drained bogs, as heretofore supposed. If the former, is the present race of *Eriophorum* on the drained peats the same as that of earlier times, and the same as that of the present Swedish marginal fens, or are different races involved, with different tolerances and requirements? It may of course be that in Britain the greater air humidity allows this plant to grow in drier habitats than in Sweden, but the problem remains of what conditions were like during the earlier *Eriophorum* phase.

Analogous problems arise in the case of *Schoenus nigricans*, which appears to be a distinct calciphile on the European continent, while growing in both calcareous and acid sites in the west of Ireland and in southern England. A possible interpretation is that the mild and equable climate of the latter regions is optimal for *Schoenus*, and allows a wide range of soil tolerance, while under a more continental climate soil preferences may determine the distribution of the species. In Britain, there also appear to be size differences in the plants of acid and alkaline habitats, but whether these are genetic or are environmentally induced is at present unknown. Similarly, *Molinia caerulea* grows very differently on ombrogenous bogs and on peats flushed by mineral soil water. In the former case it is scattered and depauperate, in the latter tall and caespitose, forming dense hummocks (Tansley, 1939). Again, the possibility of biotype differences has not been examined.

CONCLUDING REMARKS

From the foregoing pages it will be apparent that variations in a number of factors may produce the same response in vegetation and soil, and also that variation in one factor may frequently compensate for parallel variation in another. For instance, lower rainfall, warmer temperatures, more varied relief, more basic rocks, and greater human settlement all tend to inhibit or retard peat formation. On the other hand, higher rainfall may counterbalance higher temperatures (and vice versa), while marked relief or lime-rich rocks may tend to restrict peat accumulation in wet climates. It is owing to such interactions and interrelations that the problems of bog ecology, especially those concerned with the historical aspects of bog development during postglacial times, are so complex and difficult. But the student may perhaps console himself with the reflection that such complexity, by compelling a large measure of field study, is also largely responsible for the interest and fascination of the subject.

SUMMARY

An attempt is made to present (1) a reasonably straightforward account of bog development and peat accumulation as it commonly occurs in northern Britain, (2) a discussion of some chemical aspects of bog ecology, and (3) a general view of some ways in which the major ecological factors may influence the course of bog development in various parts of the world.

Under the heading of climate, the effects of rainfall, climatic fluctuation, temperature, atmospheric nutrient supply, and wind are discussed. The function of topography is made apparent in its influence upon water flow and nutrient supply. The importance of both physical and chemical aspects of the geological factor are pointed out. Under the biotic factor, human cultural operations, faunistic and

floristic differences between widely separated regions, and the possibility of subspecific differences in certain species typical of peat lands are briefly mentioned. Finally, the importance of interrelations and interactions of the factors affecting bog development is reemphasized.

ACKNOWLEDGMENTS

It is a pleasure to express my gratitude to Dr. Hugo Sjörs for much friendly criticism of this review, and especially to acknowledge my great debt to Professor W. H. Pearsall, who first encouraged me to study the ecology of peat lands, and has been an unfailing source of ideas and assistance ever since.

LIST OF LITERATURE

Auer, V. 1923. *Phragmites communis* (L.) auf den Mooren von Kuusamo und Kuolajärvi. *Ann. (bot.) Soc. zool.-bot. fenn. Vanamo*, 1: 305–320.

Barry, T. A. 1954. Some considerations affecting the classification of the bogs of Ireland, and their peats. *Proc. int. Peat Symp.*, Bord na Mona, Dublin.

Boyce, S. G. 1951. Source of atmospheric salts. *Science*, 113: 620–621.

Carter, G. S. (no date) *The Papyrus Swamps of Uganda*. W. Heffer & Sons, Cambridge.

Chenery, E. M. 1952. A digest of the chemistry of dead swamps in Kigezi district, S. W. Uganda. *Ann. Rept. hydrol. Surv. Dept.*, Entebbe, Uganda.

——. 1954. Acid sulphate soils in central Africa. *Trans. 5th int. Congr. Soil Sci.*, 4: 195–198.

Clapham, A. R., and H. Godwin. 1949. Studies of the post-glacial history of British vegetation. VIII. Swamping surfaces in peats of the Somerset levels. IX. Prehistoric trackways in the Somerset levels. *Phil. Trans.*, B, 233: 233–273.

Conway, V. M. 1948. Von Post's work on climatic rhythms. *New Phytol.*, 47: 220–237.

——. 1954. Stratigraphy and pollen analysis of Southern Pennine blanket peats. *J. Ecol.*, 42: 117–147.

Darlington, H. C. 1943. Vegetation and substrata of Cranberry Glades, West Virginia. *Bot. Gaz.*, 104: 371–393.

Du Rietz, G. E. 1949. Huvudenheter och huvudgränser i svensk myrvegetation. *Svensk bot. Tidskr.*, 43: 274–309. (English summary).

——. 1950. Phytogeographical excursion to the Ryggmossen mire near Uppsala. *Excursion Guide*, A II, b 2, *Int. bot. Congr.* (Stockholm), 7.

Emanuelsson, A., E. Eriksson, and H. Egner. 1954. Composition of atmospheric precipitation in Sweden. *Tellus*, 3: 261–267.

Eriksson, E. 1955. Air-borne salts and the chemical composition of river waters. *Tellus*, 7: 243–250.

Früh, J. 1897. Ueber Moorausbrüche. *Vjschr. naturf. Ges. Zürich*, 42: 202–237.

Godwin, H. 1946. The relationship of bog stratigraphy to climatic change and archaeology. *Proc. prehist. Soc.*, no. 1.

——. 1949. Studies of the post-glacial history of British vegetation. X. Correlation between climate, forest composition, prehistoric agriculture and peat stratigraphy in sub-boreal and sub-atlantic peats of the Somerset levels. *Phil. Trans.*, B, 233: 275–286.

——, and M. H. Clifford. 1938. Studies of the post-glacial history of British vegetation. I. Origin and stratigraphy of fenland deposits near Woodwalton, Hunts. II. Origin and stratigraphy of deposits in southern fenland. *Phil. Trans.*, B, 229: 323–406.

Gore, A. J. P., and S. E. Allen. 1956. Measurement of exchangeable and total cation content for H^+, Na^+, K^+, Mg^{++}, Ca^{++}, and iron, in high level blanket peat. *Oikos*, 7: 48–55.

Gorham, E. 1950. Variation in some chemical conditions along the borders of a *Carex lasiocarpa* fen community. *Oikos*, 2: 217–240.

——. 1953a. Some early ideas concerning the nature, origin and development of peat lands. *J. Ecol.*, 41: 257–274.

——. 1953b. Chemical studies on the soils and vegetation of waterlogged habitats in the English Lake District. *J. Ecol.*, 41: 345–360.

——. 1953c. A note on the acidity and base status of raised and blanket bogs. *J. Ecol.*, 41: 153–156.

——. 1955a. On the acidity and salinity of rain. *Geochim. et cosmoch. Acta*, 7: 231–239.

——. 1955b. On some factors affecting the chemical composition of Swedish fresh waters. *Geochim. et cosmoch. Acta*, 7: 129–150.

——. 1956a. The ionic composition of some bog and fen waters in the English Lake District. *J. Ecol.*, 44: 142–152.

——. 1956b. On the chemical composition of some waters from the Moor House nature reserve. *J. Ecol.*, 44: 377–384.

——, and A. V. Gorham. 1955. Iron, manganese, ash and nitrogen in some plants from salt marsh and shingle habitats. *Ann. Bot., Lond.*, N.S., 19: 571–577.

——, and W. H. Pearsall. 1956a. Acidity, specific conductivity, and calcium content of some bog and fen waters in northern Britain. *J. Ecol.*, 44: 129–141.

——, and ——. 1956b. Production ecology. III. Shoot production in *Phragmites* in relation to habitat. *Oikos*, 7: 206–214.

Granlund, E. 1932. De svenska högmossarnas

geologi. *Sverig. geol. Unders. Afh.*, Ser. C, No. 373. (Germany summary).

HEDBERG, O. 1954. A pollen-analytical reconnaissance in tropical East Africa. *Oikos*, 5: 137–166.

HESLEP, J. M. 1951. A study of the infertility of two acid soils. *Soil Sci.*, 72: 67–80.

JENNY, H. 1951. Contact phenomena between adsorbents and their significance in plant nutrition. In *Mineral Nutrition of Plants*, (E. Truog, ed.). University of Wisconsin Press, Madison.

KELLER, W. D., and A. F. FREDERICKSON. 1952. Role of plants and colloidal acids in the mechanism of weathering. *Amer. J. Sci.*, 250: 594–608.

KELLOGG, C. E., and I. J. NYGARD. 1951. Exploratory study of the principal soil groups of Alaska. *Agric. Monogr.*, No. 7.

KIVINEN, E. 1938. Die Moorböden Finnlands. *Agrogeol. Medd.*, 47: 18–30.

KULCZYNSKI, S. 1949. Peat bogs of Polesie. *Mem. Acad. Sci. Cracovie*, Classe Sci. math. et nat., B, No. 15.

LAMBERT, J. M. 1953. The past, present and future of the Norfolk Broads. *Trans. Norfolk Norw. Nat. Soc.*, 17: 223–258.

LIND, E. M. 1954. In *Papyrus Swamps of Uganda*, a symposium of the British Ecological Society, Jan. 6, 1954, reported in *J. Ecol.* 52: 585–587.

LUNDQVIST, G. 1943. Norrlands jordarter. *Sverig. geol. Unders. Afh.*, Ser. C, No. 457.

MALMER, N., and H. SJÖRS. 1955. Some determinations of elementary constituents in mire plants and peat. *Bot. Notiser*, pp. 46–80.

MALMSTRÖM, C. 1923. Degerö Stormyr. *Medd. Skogsförsöksanst. Stockh.*, 20. (Germany summary).

——. 1931. Om faran för skogsmarkens försumpning i Norrland. *Medd. Skogsförsöksanst. Stockh.*, 26. (Germany summary).

——. 1952. Svenska gödlingsförsök för belysande av de näringsekologiska villkoren för skogsväxt på torvmark. *Commun. Inst. for. Finl.*, 40.

MATTSON, S., and N. KARLSSON. 1944. The pedography of hydrologic soil series. VI. The composition and base status of the vegetation in relation to the soil. *LantbrHögsk. Ann.*, 12: 186–203.

——, and E. KOUTLER-ANDERSSON. 1954. Geochemistry of a raised bog. *LantbrHögsk. Ann.*, 21: 321–366.

——, G. SANDBERG, and P.-E. TERNING. 1944. Electrochemistry of soil formation. VI. Atmospheric salts in relation to soil and peat formation and plant composition. *LantbrHögsk. Ann.*, 12: 101–118.

MAYER, A. M., and E. GORHAM. 1951. The iron and manganese content of plants present in the natural vegetation of the English Lake District. *Ann. Bot., Lond.*, N.S., 15: 247–263.

MILLINGTON, R. J. 1954. *Sphagnum* bogs of the New England plateau, New South Wales. *J. Ecol.*, 42: 328–344.

MITCHELL, R. L. 1954. Trace elements in Scottish peats. *Proc. int. Peat Symp.*, Bord na Mona, Dublin.

MÖLDER, K., and M. SALMI. 1955. The general geological map of Finland, sheet B. 3, Vaasa. Explanation to the map of superficial deposits.

MOORE, J. J. 1954. Irish bog ecology: its role and development. *Proc. int. Peat Symp.*, Bord na Mona, Dublin.

NEWBOULD, P. J., AND E. GORHAM. 1956. Acidity and conductivity measurements in some plant communities of the New Forest valley bogs. *J. Ecol.*, 44: 118–128.

NICHOLS, G. E. 1918. The vegetation of northern Cape Breton Island, Nova Scotia. *Trans. Conn. Acad. Arts Sci.*, 22: 249–467.

OLSEN, C. 1950. The significance of concentration for the rate of ion absorption by higher plants in water culture. *C. R. Lab. Carlsberg*, Ser. Chim., 27: 291–306.

OSVALD, H. 1923. Die Vegetation des Hochmoores Komosse. *Svenska Växtsoc. Sällsk. Handl.*, 1.

——. 1949. Notes on the vegetation of British and Irish mosses. *Acta phytogeogr. suec.*, 26.

OVINGTON, J. D. 1956. The composition of tree leaves. *Forestry*, 29: 22–28.

PEARSALL, W. H. 1918. The aquatic and marsh vegetation of Esthwaite Water. *J. Ecol.*, 6: 53–74.

——. 1938. The soil complex in relation to plant communities. II. Characteristic woodland soils. III. Moorlands and bogs. *J. Ecol.*, 26: 194–209 and 298–315.

——. 1950. *Mountains and Moorlands*. Collins, London.

——, and E. GORHAM. 1956. Production ecology. I. Standing crops of natural vegetation. *Oikos*, 7: 193–201.

——, and E. M. LIND. 1941. A note on a Connemara bog type. *J. Ecol.*, 29: 62–68.

——, and C. H. MORTIMER. 1939. Oxidation-reduction potentials in waterlogged soils, natural waters and muds. *J. Ecol.*, 27: 483–501.

POST, L. VON, and R. SERNANDER. 1910. Pflanzenphysiognomische Studien auf Torfmooren in Närke. *Excursion Guide*, A 7, *Int. Geol. Congr.* (Stockholm), 11.

POTZGER, J. E. 1934. A notable case of bog formation. *Amer. midl. Nat.*, 15: 567–580.

——, and A. COURTEMANCHE. 1955. Permafrost and some characteristics of bogs and vegetation in northern Quebec. *Rev. Canad. Geogr.*, 9: 109–114.

PUUSTJÄRVI, V. 1952. The precipitation of iron in peat soils. *Suom. Maataloust. Seur. Julk.*, 78, 1.

——. 1955. On the colloidal nature of peat-forming mosses. *Arch. Soc. zool.-bot. fenn. Vanamo*, Suppl., 9: 257–272.

RANKAMA, K., and T. G. SAHAMA. 1950. *Geochemistry*. University of Chicago Press.

RIGG, G. B., and P. D. STRAUSBAUGH. 1949. Some stages in the development of *Sphagnum* bogs in West Virginia. *Castanea*, 14: 129–148.

ROIVAINEN, H. 1954. Studien über die Moore Feuerlands. *Ann.* (*bot.*) *Soc. zool.-bot. fenn. Vanamo*, 28, No. 2.

ROMELL, L.-G., and S. O. HEIBERG. 1931. Types of humus layer in the forests of northeastern United States. *Ecology*, 12: 567–608.

SALMI, M. 1950. Turpeiden hivenaineista. *Geotekn. Medd.*, 51.

——. 1955. Prospecting for bog-covered ore by means of peat investigations. *Bull. Comm. geol. Finl.*, No. 169.

SJÖRS, H. 1948. Myrvegetation i Bergslagen. *Acta phytogeogr. Suec.*, 21. (English summary).

——. 1950a. On the relation between vegetation and electrolytes in north Swedish mire waters. *Oikos*, 2: 241–258.

——. 1950b. Regional studies in north Swedish mire vegetation. *Bot. Notiser*, pp. 173–222.

SUGAWARA, K., S. OANA, and T. KOYAMA. 1949. Separation of the components of atmospheric salt and their distribution. *Bull. chem. Soc. Japan*, 22: 47–52.

TAMM, C. O. 1951. Chemical composition of birch leaves from drained mire, both fertilized with wood ash and unfertilized. *Svensk. bot. Tidskr.*, 45: 309–319.

——. 1954. Some observations on the nutrient turnover in a bog community dominated by *Eriophorum vaginatum* L. *Oikos*, 5: 189–194.

TAMM, O. 1950. *Northern Coniferous Forest Soils*. Scrivener Press, Oxford.

TANSLEY, A. G. 1939. *The British Islands and Their Vegetation*. Cambridge University Press, Cambridge.

TOLPA, S. 1947. Biologia torfowiska wysokiego "Mchy Jelnienskie" kolo Dzisny na Wilenszczyznia. *Roczn. Lakowy Torfowy*, 3: 1–62. (English summary).

VLAMIS, J. 1949. Growth of lettuce and barley as influenced by degree of calcium saturation of the soil. *Soil Sci.*, 67: 453–466.

WAKSMAN, S. 1936. *Humus*. Williams and Wilkins, Baltimore.

——. 1942. The peats of New Jersey and their utilization. *Bull. Dept. Conservation and Development*, State of New Jersey, Geol. Ser., No. 55.

——, and K. R. STEVENS. 1929. Contribution to the chemical composition of peat. V. The role of micro-organisms in peat formation and decomposition. *Soil Sci.*, 28: 315–340.

WEBB, D. A. 1947. The vegetation of Carrowkeel, a limestone hill in N. W. Ireland. *J. Ecol.*, 35: 105–129.

WIKLANDER, L., and G. HALLGREN. 1949. Studies on gyttja soils. I. Distribution of different sulfur and phosphorus forms and of iron, manganese, and calcium carbonate in a profile from Kungsängen. *LantbrHögsk. Ann.*, 16: 811–827.

——, G. HALLGREN, N. BRINK, and E. JONSSON. 1950. Studies on gyttja soils. II. Some characteristics of two profiles from northern Sweden. *LantbrHögsk. Ann.*, 17: 24–36.

WITTING, M. 1947. Katjonbestämningar i myrvatten. *Bot. Notiser*, pp. 287–304. (English summary).

——. 1948. Fortsatta katjonbestämningar i myrvatten sommaren 1947. *Svensk bot. Tidskr.*, 42: 116–134. (English summary).

WOODCOCK, A. H., C. F. KIENTZLER, A. B. ARONS, and D. C. BLANCHARD. 1953. Giant condensation nuclei from bursting bubbles. *Nature, Lond.*, 172: 1144–1145.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief yet critical indications of the character, content, and value of new books in all of the various fields of biological interest. Longer reviews will be accorded books of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to H. B. Glass, Associate Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

GENETIC VARIABILITY IN POPULATIONS

BY C. C. LI

Graduate School of Public Health, The University of Pittsburgh

A Review of POPULATION GENETICS: *The Nature and Causes of Genetic Variability in Populations. Cold Spring Harbor Symp. quant. Biol., Vol. XX.*

The Biological Laboratory, Cold Spring Harbor, N. Y. $8.00. xvi + 346 pp. + 3 pl.; text ill. 1956.

The 1955 proceedings of the Cold Spring Harbor Symposium signifies the adolescence of population genetics. There were 196 geneticists, statisticians, and animal and plant breeders attending, among whom were 40 visitors from abroad. Thirty-two papers were presented in one week's time. Generally speaking, the first few days were devoted to theoretical and statistical developments and the last few days to experimental findings. Each group of three or four loosely related papers was followed by a "synthesis" winding up the day's business.

Komai's opening speech is reproduced in full in Demerec's foreword. In the first main paper, Dobzhansky discusses some very fundamental points of population genetics. His topics include: the adaptive norm, the balance hypothesis, two kinds of mutational load, errors of selection, and the internal genetic cohesion of a mendelian population. Wright emphasizes once again the concept of evolution as something that emerges by trial and error processes from states of approximate equilibrium. Such a process is favored by balance among the evolutionary factors rather than by extreme action of any single factor. Then he makes a distinction between the intrademic (internal) selective value V_I and the interdemic (external) selective value V_E of a population. Dempster describes several devices of maintaining alleles at intermediate frequencies in a population; he points out that selection pressures which vary in space or time could maintain genetic variance of fitness with a substantial additive component, and that heterozygote superiority is not always necessary. Kimura deals with the stochastic process which leads to a steady-state distribution of gene frequencies under the joint effect of systematic pressures and random fluctuations, the latter including not only the ordinary error of sampling of gametes but also the effect of random fluctuation of the selection intensity. This is a major mathematical advance in theoretical genetics. Unfortunately, as Wright remarked, we probably will have to puzzle for a long time before the full significance of Kimura's paper can be appreciated. Malecot has added a brief note on the decrease of genetic relationship with distance. It was Crow's task to summarize these papers and he has done a splendid job of it, in showing the relationship between some of the mathematical expressions of different authors.

Kempthorne presents a comprehensive review and extension of the methods of analyzing the genetic variance into different components, expressing the covariance between relatives in terms of these components, and thus obtaining the correlation between relatives under random mating. The fundamental technique here is based on the analogy between a genotype and a "treatment" in factorial experiments. Hayman presents quite a different method of describing and analyzing gene action and interaction. His fundamental trick is to take a variable $\theta = +1, 0, -1$ for the genotypes AA, Aa, aa, respectively. The trouble is that this device cannot deal with multiple alleles or selection problems, both of which are vital subjects in population genetics. The author pleads: "Any suggestions would be welcome." In his paper, Sprague reports that continued selection for high oil content in corn for 50 years still shows improvement, although the low oil series has slowed down after 20 years of selection. His explanation is that the failure of response to selection is not necessarily due to the lack of genetic variability, but

may be due to inadequate experimental techniques. Comstock has not only digested these papers for the reader but also gives a lucid explanation of the meaning of genotypic variance and shows why their empirical estimates are usually biased to an unknown degree. With respect to the mathematical articles he says: "There is much of value to be learned by converting the symbolic expressions into arithmetic values assuming specific genetic models." In this connection, I recall that Karl Pearson used to require all his students to give at least one numerical example in their mathematical papers.

Manning reports that all the present commercial cotton in Uganda is descended from a single outstanding plant selected in 1935, yet selection gives continued improvement in yield for all these years. This is positive evidence for the persistence of genetic variability, and Manning entertains several possible explanations. Haskell describes the complicated genetics of the blackberry. It is a fine piece of description, illustrated by graphs, polygonal diagrams, correlation diagrams, pictorial scatter diagrams, etc., by which one can judge which plants are apomicts and which arose sexually. Robinson's and Comstock's experiments on crossing and selection in corn represent the nearest combination yet of a mathematical model and an experimental design. Even so, the interpretation of the results are by no means certain, and more critical experiments have already been planned. Sakai's reports on the competitive ability (a genetic character) of barley and rice is very informative. He found that the F_1 barley hybrids are more vigorous when grown by themselves, but are usually poor competitors when grown with parent strains. Diploid plants are better competitors than their tetraploid derivatives are, but the amphidiploid sometimes shows greater competitive ability than the parental species. No morphological character has been found to be correlated with competitive ability. The root system, however, has not been examined. Mather, in synthesis, makes a general survey of the selection results and the principles involved. The response to selection must depend on three sets of factors: (a) the types and intensities of the selective forces themselves; (b) the gene action and interaction and genotype-environment interaction in producing the phenotype; and (c) the amount, distribution, and system of genetic variability in the population. Mather makes the important distinction between the drastic, short-term artificial selection utilizing the existing variability, and the slow, long-term natural selection which leads to new systems of variability. He further points out that developmental homeostasis is not an innate property of heterozygosis, and heterozygotes are not always more stable in development; the stability is a result of selection, a view shared by several other authors, e.g., Thoday.

Forbes Robertson reports the results of selection for body size in *Drosophila*. He obtained the familiar asymmetrical response—selection for small size produces a greater change than does selection for large size. When established large strains are intercrossed, selection among their progeny results in new response, and the body size becomes larger than the originally established level. Similar selection on intercrossed small lines has no response. This and other results lead him to think that the genes for smaller size are hypostatic to those for normal size. Falconer reports two-way selection results in mice. The response is again asymmetrical, to different degrees in different characters. The asymmetry is thought to be due to natural selection opposing continued change toward extreme size. This interpretation is different from that which Falconer offered in the Pavia symposium of 1953. He himself said: "Deductions from the results of selection experiments must be regarded as provisional and we must recognize the element of personal judgment." This shows the desperate need for more critical experimental designs. Bell, Moore, and Warren try to give an evaluation of some of the methods used for the improvement of quantitative traits. Dickerson discusses the problems of selection for multiple objectives. Alan Robertson, in synthesis, reiterates the point that cessation of response to selection does not necessarily mean genetic fixation. This maintenance of genetic variability perhaps occurs as a result of a balance between the characters selected for and the fitness components. In such situations, heritability estimates are useless in predicting response to selection.

Ford, in studying the butterflies of the Scilly islands, concludes that butterflies in small islands are adjusted by selection to the distinctive ecology of their respective habitats, while those in large islands can be adapted only to the average conditions which obtain there. Among factors which make rapid evolution possible, he also mentions the effects of fluctuations in numbers, allopolyploidy in plants, polyploidy in animals (hamster, wasp, moth), migration, etc. He notes that industrial melanism, though a striking phenomenon in England, has not been studied in the United States. (Frankly, I do not know what is the situation in the world-capital of heavy industry, the melanic city of Pittsburgh.) Ford believes that polymorphism is associated with close linkage ("super-genes"), such as in the Rh series. He goes further, to say: "There is little doubt in my mind that the ABO system, still regarded as controlled by a series of multiple allelomorphs, will be added to them." Time will tell. Allison gives a review of the evidence for heterozygote superiority in maintaining polymorphism in man, and is certainly the man to speak with full authority about sickle cell trait, sickle cell anemia, and the resistance to falciparum malaria in Africa. His case was brilliantly presented. Allison predicts that the sickle cell gene in the American Negro population must be losing ground and that the polymorphism is in a transient state here. He is very probably right on this point. In discussing the poly-

morphism of human blood groups, however, he asserts that the Rh-positive individuals are gradually replacing the Rh-negative individuals in western Europe. Apparently he is not aware that there are geneticists who have reason to think that the Rh-negative gene may actually be increasing in frequency. Unfortunately, this is one of those slow, long-term selection problems for which we will probably have to wait a long time before we can definitely say which way the gene frequency (Rh) is going. Since reproductive patterns and environmental conditions control both the nature and the location of the equilibrium and since they are constantly changing themselves, maybe the Rh frequency is not going anywhere at all—just wandering around. Allison, like Ford, also believes that the ABO system is controlled by a "super-gene." Ceppellini, in discussion, presented some very interesting data on thalassemia minor in Sardinia and showed that its frequency is also influenced by environmental conditions (i.e., is subject to selection). Therefore he warns against the uncritical use of blood groups in anthropology. Stone is one of the authorities on chromosomal reorganizations with in the genus *Drosophila*. The usual belief is that the extent of chromosome polymorphism is directly correlated with the extent of environmental diversity. Thus, the desert species seldom have an appreciable chromosome polymorphism. However, Stone points out that this does not mean that evolution cannot go on. The *repleta* group, with many desert species, has actually evolved into the largest species group in *Drosophila*. Many other successful species have also achieved their adaptive versatility without cytological polymorphism. Stone's conclusion is that although cytological modifications are often important in evolution, the fundamental changes have been in the organization of different balanced gene systems. This point has important bearings on the papers that were presented on the following day of the symposium. Sheppard, in synthesis, expressed the hope that more attention might be paid to the ecology of the populations. He mistook $\bar{W}$ as the average selective value of the genes in the population; it is, in fact, the average selective value of the genotypes within a population. One of the applications of $\bar{W}$ has been illustrated, though crudely, by Allison's Fig. 1.

Carson reported that populations at the edge or margin of the range of certain *Drosophila* species appear to possess more freedom for gene recombination than the populations in the center of the species range. The central populations with a high degree of chromosomal polymorphism suffer a drastic reduction in their ability to undergo recombination by crossing over, whereas the marginal populations, with fewer inversions, have relatively more free crossing over and thus a higher evolutionary potential. They "act as scouts" for the species, as Dobzhansky puts it. But the general picture is not very clear as to which—areal distribution or inversions—is the cause and which is the effect. Nicholson seems to be unable to disassociate the meaning of a word in common usage from that technically defined. The following non-random sample quotations are intended to show the effect of semantic difficulties: "There is no factual evidence that organisms really fit their environments. . . . It is unnecessary to postulate that they do so in order to account for evolution. . . . The primary result of selection is not the production of adaptation, as is generally supposed, for before selection took place the species was already adapted, in the sense of being suitable to live in the given environment. . . ." Prevosti finds that wing length of *Drosophila* decreases with geographical distribution from north to south in the British Isles. He concludes that wing length is an adaptive trait. Buzzati-Traverso, in discussing the fitness of a population, emphasizes correctly that the problem is that of measuring such value. He makes some suggestions as to how the absolute measure of fitness of two separate populations may be obtained, assuming identity of environment.

Wallace and Vetukhiv studied the viability (percent survival of larvae) and fecundity (eggs per day and eggs per lifetime) of four *Drosophila* species and of crosses between them. The vast majority of the differences observed are ascribed to the individual combinations rather than to either of two chromosomes of the combinations. The major conclusion is that all local gene pools have been integrated by selection. This renders the concept of a single wild-type or "normal" genotype of a species untenable. King reported that the F_1 of two lines of *D. melanogaster* resistant to DDT showed the same mean tolerance as the parental lines, but that the F_2 is of lower mean tolerance and greater variance. Surprisingly, the F_3 shows a mean tolerance as high as that of F_1 again. King thinks this may be due to differential fertility among the F_2 individuals. Thoday's results point to the view that heterozygosity *per se* is not the essential cause of developmental flexibility (homeostasis), but rather that favorable heterozygous combinations occur as a result of the coadaptation of homologous chromosomes within populations. This coincides with the view expressed by Mather earlier in the symposia. This view does not necessarily exclude that of heterotic loci; both might be true in different cases. Mayr, in synthesis, has really put the concept of the integration of gene pools into a nutshell (or soup tureen); a gene product which when added as ingredient to one "developmental soup," greatly enhances its "goodness," but, when placed in a different "soup," merely "spoils the broth." Lerner, entrusted to do the concluding survey of the Symposium, as usual excelled and displayed an extraordinary faculty for organizing and crystallizing ideas. He has both surveyed the forest and examined the trees. His summary is the best review of the volume.

Some very brief general comments: The need for a precise definition of some of the current terms and the need for creating new terms have both been pointed out

by Mayr. I am surprised to find that even the thirty-year-old term "unstable equilibrium" has been used in an entirely different and unrelated sense. "Heritability" has acquired more and more different meanings. Before a uniform terminology can be agreed upon, each author should indicate what he means when he uses a term. That is the least to require. I admit the right of scientists to invent new words when necessary, such as "fissionable" in nuclear physics. But I doubt if "plateaued population" and "combinability" are really necessary.

I fully realize how difficult it is to avoid typographical errors in a volume like this. But this volume seems to have more than usual, especially in the few mathematical papers. Some of the errors have even acquired a mendelian flavor. Since we regard *Aa* and *aA* as the same genotype, we have no difficulty in figuring out that "yb" is "by" and "ot" is "to." Recalling that in XO organisms the Y chromosome is missing, we conclude that "wh" could be "why" and "ma" could be "may." There is always a small amount of mutation, of course. Thus, the hemoglobin gene Hb^A in one paper becomes H^N in another (and this is not a typographical error).

I would like to mention just one more thing. Although it has nothing to do with the presented papers, I think it nevertheless contributed a great deal to the general success of the symposium. Whether a reflection of a limited budget or not, Demerec has furnished his new auditorium with three kinds of chairs: the most comfortable ones in the front, the ordinary ones in the middle, and some small, hard, cheap chairs in the back. The result is marvelous, if you understand what is meant.

REVIEWS AND BRIEF NOTICES

General Biology: Philosophy and Education.....170
Biology: History and Biography.....171
The Young Naturalist.....172
Ecology and Natural History.....173
Evolution.....177
Genetics and Cytology.....180
Plant Physiology.....182
Economic Botany.....182
General and Systematic Zoology.....184
Economic Zoology.....191
Animal Morphology.....192
Animal Physiology.....194
Animal Nutrition.....195
Biophysics and General Physiology.....196
Biochemistry.....196
Microbiology.....199
Health and Disease.....202
Psychology and Animal Behavior.....205
Human Biology.....210
Biometry.....214
De Omnibus Rebus et Quibusdam Aliis.....215

GENERAL BIOLOGY: PHILOSOPHY AND EDUCATION

LIFE SCIENCE. *A College Textbook of General Biology. By Thomas S. Hall and Florence Moog. John Wiley & Sons, New York; Chapman & Hall, London.* $6.50. x + 502 pp.; ill. 1955.

Choosing a textbook for an introductory course in biology or zoology is no longer a simple task. Each academic year ushers in several new books, and the rate seems to be accelerating. Such a wealth of material poses a series of Hobson's choices; each book has so many good features that a final decision is hard to render. If any trends exist, I would say that they run toward (a) attractiveness in illustration, layout, binding, and type, (b) readability, the informal, discursive style, and (c) more physiology and biochemistry and less systematics. Whether these trends be correctly assessed or not, certainly *Life Science* reflects all three. As regards the first of these trends one cannot complain that the drawings sacrifice accuracy for dramatization. With but one or two exceptions, this weakness has been avoided. Readability is also praiseworthy so long as accuracy is not forsaken. In the present instance, several misstatements were noted, and one wonders whether these may have not resulted from the effort to achieve an informal style. As to the third trend, this book will please you more if you prefer the physiological, adaptational approach rather than the morphological, descriptional. Classification as such is omitted; the space devoted to a survey of the plant and animal kingdoms is small (it should be pointed out that most of the material is zoological). Most of the errors that were detected were in the systematic portion of the book, and while this review is not the place to itemize them, two of them should be mentioned because of their conspicuousness. Figure 5.8, labelled an ostracoderm, is actually a placoderm; a footnote (p. 198) states that "a few reptiles . . . have internal fertilization."

This book has definitely accomplished the difficult task of presenting the significant data of biological science. A noteworthy feature is the inclusion in the text of brief insights into the historical background of the discoveries, refinements, and methods upon which our present hypotheses and deductions are based.

HENRI C. SEIBERT

BIOLOGY: HISTORY AND BIOGRAPHY

A Historical Review of the Mollusks of Linnaeus. *Part 4. The Genera Buccinum and Strombus of the Class Gastropoda. Bull. Amer. Mus. nat. Hist., Vol. III, Art. 3.*

By Henry Dodge. American Museum of Natural History, New York. $2.00 (paper). Pp. 153–312. 1956.

This is another installment of Henry Dodge's study of the Linnaean genera and species. Since zoological nomenclature begins with Linnaeus, every generic and specific name given by him, as well as every type designation that can be traced to Linnaeus' work, is available in the literature if it can be recognized. When we recall how modern research has divided every one of the Linnaean genera into several dozen new ones, we can understand the importance of identifying correctly as many of the Linnaean nomenclatorial terms as possible.

In 1958, the bicentenary of the tenth edition of the *Systema Naturae* will be celebrated throughout the scientific world, but no single contribution to any celebration is likely to be more helpful than Henry Dodge's *Historical Review*.

The present number is devoted to the genera *Buccinum* and *Strombus*. The former is an excellent example of the need for such a work as Dodge's, since among the Linnaean species originally assigned to the genus *Buccinum* are some half a dozen that are now the legitimate types of genera later established, in as many families (*Terebra*, *Harpa*, *Tonna*, *Nassarius*, etc.) not especially closely related. In the thirteenth edition of the *Systema Naturae*, edited by Gmelin, this number seems to have increased.

On the other hand, the genus *Strombus*, although also broken up, is still largely confined to the family Strombidae. In other words, the Linnaean genus *Strombus* was not a heterogeneous collection of miscellaneous species, but a natural group, though of more than generic value as genera are construed today.

The large and detailed bibliography and the systematic index accompanying Dodge's work will be found most helpful. Only one error was detected by the reviewer. Some of the publications by Maxwell Smith are said to be mimeographed, whereas actually they were reproduced by offset printing.

Joshua L. Baily, Jr.

Greek Science in Antiquity.

By Marshall Clagett. Abelard-Schuman, New York. $4.75. xii + 217 pp. + 4 pl.; text ill. 1955.

For some time there has been a need for a short history of Greek science, which, though based on the sources, would also take note of the more recent researches on this subject. Marshall Clagett, who teaches the history of science at the University of Wisconsin, has produced such a work.

The book is divided into two major sections. Part One is concerned with the origins of science in antiquity. Its roots in the civilizations of Egypt and Mesopotamia are pointed out, and its course is traced through the golden ages of Greek culture which flourished on the Greek mainland, the land mass of hither Asia, the Mediterranean islands, North Africa, and finally Sicily and the Italian boot. The account includes discussions of the lives and work of such familiar figures as Thales, Anaximander, Hippocrates, Aristotle, Euclid, Archimedes, Hipparchus, and Galen.

With the opening of the Christian Era in the Roman world, the author develops, in the second part of his book, the story of the fate of Greek science in late antiquity and its transformations as it passed, by way of translations into Syriac, Arabic, and Latin, into the medieval world. Among specific topics surveyed are Greek medicine and biology, mathematics, physics, and astronomy. The impact of the early Christian church on scientific thought is discussed in some detail, and the erratic course of astrology and alchemy is also traced. The book is illustrated and includes a good bibliography and index.

The author has promised readers another book on the history of medieval science, to which the present volume makes an introduction. It will be eagerly awaited.

Morris C. Leikind

Classics of Biology.

By August Pi Suñer; authorized English translation by Charles M. Stern. Philosophical Library, New York. $7.50. x + 337 pp.; ill. 1955.

With some exceptions, those writings of biologists which were eventually to assume the status of "classics" have never been as available as the important works which marked significant advances in the development of mathematics, chemistry, and physics. Perhaps this is because the importance of biological observation and research was not always immediately evident, and even the more exact findings of biologists were seen by many persons but dimly and through a vitalistic screen. More and more of these important contributions, at least significant portions of them, are becoming part of our literature of primary sources, thanks to men like Pi Suñer.

Pi Suñer's contributions to medicine and biology span more than half a century. In 1955 he received the UNESCO Kalinga Prize for scientific writing for the lay public. Even in this book, which is translated from the Spanish original, his prose retains its striking clarity.

The work is divided into 16 chapters, each centering

upon some aspect of biology or its philosophical implications. Each chapter has an introduction by Pi Suñer which is essentially historical, but which recreates the biological state of mind while setting straight the chronology of important contributions to the topic. There follows a group of selections, almost always excerpts from larger works, which represent definite advances toward a solution of the problem. Whether all of these deserve the appellation "classics" would engender some disagreement, but few would deny the value of having the selections available.

A number of chapters deal with the establishment of important biological concepts (Cell Theory, Stimulus and Excitation, Biocatalysts, Metabolism, Heredity, Geography, and Paleontology). Others consider famous biological controversies (Individual and Species, Preformation and Epigenesis). Perhaps the most interesting compilations deal with philosophical problems which are inevitably probed by biologists—Causation and Design; Reflexes, Consciousness, and Will; and The Whole and Its Parts. Here the selection of papers could not be considered unbiased, for both sides of each question are not equally developed. It is a shame, for example, to print J. S. Haldane's attack on the mechanistic theory of life without following it by F. G. Hopkins' magnificent rebuttal.

Although conceived somewhat along the same lines, there is actually very little overlap between Pi Suñer's work and Gabriel and Fogel's *Great Experiments in Biology* (*Q.R.B.*, 31:36. 1956). Either volume might be used as auxiliary reading for a good general biology course; however, they would be perhaps more useful in senior level, integrative, seminar-type courses. Together these two collections provide a satisfying diet of the best in biological writing and thought, from Aristotle to Dobzhansky.

FRANK C. ERK

THE LEGACY OF SIGMUND FREUD.
By Jacob A. Arlow. International Universities Press, New York. $2.00. vi + 96 pp. + 1 pl. 1956.

This monograph grew out of Jacob Arlow's labor of love in collecting Freud memorabilia for the centenary of his birth. It provides a brief biography of Freud's scientific development and describes his original contributions to psychiatry.

In his introduction, the author disarms his critics with a disclaimer of any serious intent to evaluate Freud's position in the scientific heavens, though he clearly regards him as a luminary of the very first order. This very failure, however, limits the usefulness of this monograph for the biologist.

Those interested in an exposition of Freud's ideas will do better to purchase Freud's *New Introductory Lectures on Psychoanalysis*. Those wondering about the scientific validity of psychoanalytic theory will find little in this volume and will have to turn to current psychologic and psychiatric journals. Those concerned with Freud's personal development will do better to look to Jones' biography for a picture of Freud through the eyes of a disciple.

An idolator of the great man, Arlow finds the touch of genius in all that the master has done. He suggests that Freud should be given credit, along with Waldeyer and Cajal, for the neurone doctrine. Unless it can be shown—and I am aware of no evidence to this effect—that Freud's early histological studies played an important part in the battleground of neurological ideas, their mere publication entitles their author to no such major position. We ascribe to Freud a revolutionary role in psychology, not only because his ideas were germinal, but also because he had the perseverance, the self-conviction, the sense of timing, and the pedagogic skill to channel his ideas into the main stream of scientific thought so as to influence its course in a major way. It can be pointed out that Schopenhauer (and others) had anticipated many of the Freudian dichotomies, and yet we properly point to Freud, not to other thinkers, as their progenitor.

Freud was, indeed, a great man, but we are—or should be—long past the stage when mere citation of the great man's words suffices. The extremely important task of examining psychoanalytic theory by scientific methods stands before us as a major challenge of the current era.

LEON EISENBERG

THE YOUNG NATURALIST

WONDER WORLD OF MICROBES.
By Madeleine P. Grant; illustrated by Clifford N. Geary. Whittlesey House; McGraw-Hill Book Company, New York, Toronto, and London. $2.75. 160 pp.; ill. 1956.

This seems to be a sort of "beginner's first book" in microbiology. The text is simple and clear, and there is an abundance of good illustrations. Industrial and food microbiology, as well as medical microbiology, receive attention. At a guess, it might be very suitable for intelligent pupils in about the seventh or eighth grade.

The text is enlivened with a considerable number of experiments which can be done either at home or in school. The growth of molds is demonstrated by wetting one of a pair of old shoes and storing both in a dark, warm closet side by side. After a week (if conditions are right), the test shoe will show a growth of mold, while the control shoe is supposed not to.

The experiments on yeast fermentation ought to work fairly well, but the unaided attempt to grow the hay bacillus (*Bacillus subtilis*) and to examine it with

the microscope is likely to be only partially successful, at best. I can remember only too well an early attempt to use a compound microscope without instruction (while studying science in the attic at the age of 14), and my complete failure to see anything at all, except with the low-power lenses. However, experiments always have some value, even if they are not invariably successful. Keeping this in mind, the book can be recommended.

WALTER C. TOBIE

ECOLOGY AND NATURAL HISTORY

ARCTIC RESEARCH. *The Current Status of Research and Some Immediate Problems in the North American Arctic and Subarctic. Spec. Pub. No. 2, Arctic Inst. N. Amer.*

Edited by Diana Rowley. The Arctic Institute of North America, Montreal. $3.50; $3.00 (members). 261 pp. + 1 folded map; ill. 1955.

The subtitle of this volume aptly describes its contents. Comprised of 26 papers submitted by selected authors, it ranges widely in both subject matter and geographic area, and varies in presentation from a simple catalog of research problems to fact-packed reports of specific research investigations. Biologists will naturally be most interested in the middle section, which is entitled Biological Sciences and which embraces articles on limnology, marine ecology, botany, soil and agriculture, wildlife, invertebrates, and entomology. But they will also find rewarding articles in the remaining sections, on the physical and social sciences. The nature and controlling factors of the physical environment, such powerful determinants of life in this rugged region, must at least be appreciated if biological problems are to be seen in correct perspective; and human ecology and acclimatization to cold should have at least an equal claim for consideration in biology as in sociology.

It is made abundantly clear that simplifications, so handy in preliminary studies, and projections from what is known of more temperate biology no longer suffice. Complexity and "otherness" must be accepted if problems are to be viewed with scientific clarity, and if fact is to be distinguished from convenient assumption. Capricious though the choice may be, the following items which interested or impressed the reviewer will serve to illustrate the type and variety of topics considered: conditions leading to reduction of visibility through ice fog or blowing snow; the close relationship of permafrost to vegetation cover, and the significance for agriculture; extent and complexity of geodetic and geophysical research; the variety of limnological conditions and the necessity for distinguishing between alpine and arctic problems; the fascinating plankton-nekton-benthon cycle of northern waters; the dependence of animal production upon local demand; the marked variation in animal populations from year to year; the power of mosquitoes "to harry the settler, his family, and livestock to a point almost beyond endurance"; a high incidence of parasitism among both animals and humans; the complexity and variety of past culture stages; the need for an immediate and detailed study of human ecology before the evidence disappears; the inadequacy of assumptions that future settlement in the subarctic will follow the pattern of past developments in more temperate lands; the need for the earliest possible planning of settlement sites and facilities; and the need for careful consideration of duration and frequency, as well as severity, of exposure in discussing acclimatization to cold.

DOUGLAS H. K. LEE

VASTNESS OF THE SEA.

By Bernard Gorsky; translated by Alec Brown. Little, Brown & Company, Boston and Toronto. $5.00. 305 pp. + 8 pl. 1957.

This is the story of a voyage from St. Malo to Tahiti in the sloop "Moana" by "four daring Frenchmen" equipped with aqualungs, cameras and piscicidal equipment. As light reading it will do no harm, although the dialogue is a bit jejune. There are, in compensation, purple passages that the translator has struggled nobly to render. In spite of Alec Brown's apologia regarding the effort to avoid pedantry and encumbrance of the text with scientific names, zoological readers will be offended by references to the poisonous sea urchin that "sent a shower of shafts" at the passerby; the mother of pearl oysters like snails, with a cat's eye operculum; the "white sharks" that become "dogfish" in the next sentence; and similar infelicities. The diagrams of surface currents on the two track charts have amazed oceanographers. As the opening remarks clearly indicate, the primary purpose of this trip was not to "get away from it all," but to provide material for one more book.

JOEL W. HEDGPETH

VIE ET MOEURS DES INSECTES.

By Rémy Chauvin. Editions Payot, Paris. 800 fr. (paper). 223 pp. + 8 pl.; text ill. 1956.

Rémy Chauvin's *Vie et Moeurs des Insectes* is another volume in the series Bibliothèque Scientifique, which includes works in the popular style on various aspects of zoology, mostly entomology. The book commences with an essay on sight, hearing, and taste in insects, which emphasizes that one cannot assume that these functions are the same for both insects and man. This

fact is very important when one considers the subject of mimicry among insects. Movement is the subject of the next two chapters, the first of which deals with tropisms or involuntary movements, and the second with deliberate and apparently intelligent actions on the part of the insect. This leads to the question, "Can insects learn?" In this chapter, the author compares the abilities of the German roach and the white rat in making their way through labyrinthine mazes. As these experiments are conducted under highly artificial conditions, and so are open to question, the next discussion centers on the "homing instinct" such as bees show in their ability to return unerringly to their hive, or to go directly to a source of food. Migration of insects and the often elaborate structures built by certain forms (termites and ants) furnish material for the two following chapters. The volume ends with a discussion of the very controversial subject of mimicry and protective coloration.

EDWARD A. CHAPIN

RATTLESNAKES. *Their Habits, Life Histories, and Influence on Mankind. Two Volumes.*

By Laurence M. Klauber. University of California Press, Berkeley. $17.50. xlvi + 1476 pp. + 2 pl. (color); text ill. 1956.

One faces a dilemma in attempting to write a conservative review of Klauber's *Rattlesnakes* and, at the same time, to do justice to the book. These volumes will stand as one of the major landmarks in American natural history for many years to come. Through them we know probably more about the biology of rattlesnakes than about that of any other animal group (excluding the primates and a few forms of economic importance). And these volumes are not merely a compilation of the work of others. The author, by vocation an engineer and an executive in a utility company, is interested in natural history only as a hobby; yet he has made major contributions to our knowledge of these interesting genera of reptiles. Besides, the books are written in a charming style that makes for enjoyable and pleasant reading. The result is a truly extraordinary pair of volumes—an exhaustive encyclopedia of rattlesnakes.

After a short Introduction, there is a general chapter about rattlesnakes and their place among other American snakes. This is followed by a 100-page chapter on their classification and identification, with a number of keys and accounts of geographical distribution. The author suggests that this material is rather technical and should be skipped by the general reader. Klauber comments regretfully that in herpetology no recognized authority has recommended a coordinated set of common names. Happily, almost simultaneously with the appearance of his work, a committee of the American Society of Ichthyologists and Herpetologists has published a suggested list of common names for North American reptiles and amphibians which, it is hoped, will bring to these groups the same nomenclatural stability that the birds have already.

A short account of the paleontology and phylogeny of rattlesnakes is followed by a fairly extended account of their morphology, devoted largely to proportions, squamation, and color patterns. A few of the topics are as follows: interspecific comparisons of length, sexual dimorphism, ontogenetic variations, scale characters in relation to climate, physiological color changes, and hybrid color patterns.

A single chapter, of some 70 pages, is devoted to the rattle itself. It includes, besides its evolution and use, a detailed account of the rattle's functional anatomy.

Included under bodily functions are accounts of growth, longevity, life persistence (with some interesting experiments on decapitated specimens), shedding, and locomotion. Klauber recognizes four major kinds of locomotion in rattlesnakes and gives a remarkably clear discussion of sidewinding. The chapter concludes with an analysis of senses, including the fascinating thermal-change detection by the facial pits. Considerable attention is given to the effects of temperature in the chapter on behavior. There are also extensive discussions of climbing proclivities and swimming. The three final chapters of the first volume consider populations and ecology, food, and reproduction.

The second volume presents considerable material of sociological as well as biological interest. The poison apparatus, the bite and its effects, and the treatment and prevention of the bite occupy some 275 pages. It is comforting to learn that in this country deaths from snake bite, during the last twenty years, have declined from about 200 annually to less than one-quarter of that number, despite our greatly increased population.

A chapter on control and utilization reasserts a theme that has been woven through both volumes: rattlesnakes are dangerous animals; and persons who are likely to meet them, intentionally or unintentionally, should exercise sober care and restraint.

The next chapter considers the enemies of the rattlesnake and includes a summary of information on their parasites and diseases. Klauber describes the specialized defense reaction of rattlesnakes to king snakes in which the rattler arches its back, keeping its neck and tail pressed firmly to the ground, and then brings the loop down forcefully onto the king snake, like a club. Interestingly, a rattlesnake from Montana, in an area where king snakes do not occur, showed the same defense reaction. It is evoked by odor.

A fascinating chapter of about 100 pages is devoted to Indians and rattlesnakes. Their contacts with each other were most varied and extensive in the Southwest. Post-Columbian knowledge of rattlesnakes is presented

in the next chapter, which includes such topics as a history of published descriptions (the first was in 1554), etymology and semantics, insignia, and place names.

The final chapter, on Myths, Folklore, and Tall Stories, is a charming and humorous collection of anecdotes. Many are traced with consummate care to their advent, and Klauber's remarks are urbane and witty.

There is a bibliography of over 3300 citations and a detailed index of about 75 pages.

The volumes are illustrated with excellent plates and carefully executed figures. Each volume has a colored frontispiece. The usual pattern for each chapter is a discussion of the material as it applies generally to rattlesnakes, followed by summaries by species, when applicable. Klauber has had an enormous correspondence with out-of-doors people, such as park rangers, and he quotes liberally—perhaps too liberally—from them. Where it is germane, the topics are enhanced by a sophisticated statistical treatment.

If there is a general theme in this biological reference work, it may be considered to be humanistic in nature. Klauber tries, quite successfully, to elucidate the contacts between men and rattlesnakes as well as to summarize our knowledge of the snakes themselves. Additional dividends offered the reader are the pleasures of frequent smiles and occasional hearty laughs as he peruses this thoughtful, informative, and enjoyable account.

The University of California Press is also to be commended. The books are well designed and attractive, and typographical errors are rare. While $17.50 may seem a great deal to pay for a single work, it is really a very reasonable price, in these times, for 1476 large pages.

While every herpetologist will want to own the *Rattlesnakes*, I also recommend it to other biologists for diverting reading. Some experimental biologists, I am sure, will be surprised at the rigorous scholarship in this fine example of modern natural history.

ARNOLD B. GROBMAN

ECOLOGICAL STUDIES ON MAMMALS, BIRDS, REPTILES AND AMPHIBIANS IN THE EASTERN BELGIAN CONGO. *Part I. (Report No. 1 of the Lund University Congo Exped. 1951–1952). Ann. Mus. Roy. Congo Belge, Ser. 8, Sci. zool., Vol. 42.*

By Kai Curry-Lindahl. Musée Royal du Congo Belge, Tervuren, Belgium. Belg. fr. 200 (paper). 78 pp. + 23 pl.; text ill. 1956.

This compilation is not a major report, but really only an annotated list of vertebrates collected or observed in the Belgian Congo while the author was investigating the migratory and wintering habits of Palearctic birds. Many of the species are listed without comment except as to means of acquisition. Others are the subject of interesting observations and comments. The most extensive descriptions have to do with the behavior of cobras. The behavior of the spitting cobra, *Naja nigricollis*, and of the water cobra, *Boulengerina annulata*, is well described. A series of 42 plates, comprising more than half of the book, illustrates many of the ecological habitats in the eastern Congo. The reproductions are of only fair quality, but are of considerable interest nonetheless, as showing both cultivated and fallow regions, the latter ranging from dry scrub and equatorial forest up to the heaths and snow fields of the highest mountains.

BRYAN P. GLASS

THE BIRDS OF LINCOLNSHIRE. *Lincolnshire Natural History Brochure No. 2.*

By A. E. Smith and R. K. Cornwallis. Lincolnshire Naturalists' Union, Lincoln. 8s. (paper); 16s. (cloth). 136 pp. + 1 folded map + 5 pl.; text ill. 1955.

Lincolnshire, in east-central England, borders on the North Sea. It is second only to Yorkshire in size and yet is one of the most remote and least known of the English counties. In the present work the history of this area and that of its birds is described. A map, reconstructed to show the principal bird habitats that existed around 1750, shows a large extent of heath and fen, with scattered woodlands. The changes that have taken place since that time are all familiar ones—principally the drainage of the wetlands for agriculture and the afforestation of softwoods. The effect of these alterations of habitat on the birds is discussed. The migration pattern of the region is analysed, the history of ornithology in Lincolnshire is summarized, and a bird list, with critical comments, is given. This list includes 225 species, with 28 additional subspecies. The status of all these forms, past and present, is recorded. There is a bibliography and a large insert map of present-day habitats. In sum, this is what I would call an ideal local check-list. Its pattern could well be copied.

HENRI C. SEIBERT

MAMMALS OF COAHUILA, MÉXICO. *Univ. Kansas Pub. Mus. nat. Hist., Vol. 9, No. 7.*

By Rollin H. Baker. University of Kansas, Lawrence. Free upon request (paper). Pp. 125–335; ill. 1956.

Anyone interested in the ecological distribution of the vertebrate fauna of Mexico will find this volume an indispensable addition to his library. Rollin Baker has surveyed Coahuila, collecting mammals from all parts

of the state, and soliciting much information concerning the rarer species from local inhabitants. From his own observations, and from published accounts of plant and animal ecologists, geologists, and climatologists, he has set an ecological stage upon which his characters, the Coahuila mammals, parade in orderly and understandable fashion.

Baker recognizes Merriam's life-zones as most satisfactorily representing the major biotic divisions of the state, ascending from the Lower Sonoran Zone at the lowest elevations to the Canadian Zone upon the highest mountain peaks. Within these major zones he uses Muller's vegetation types in describing the variations in habitat that so greatly influence mammalian distribution. In the text each of these types is described, and the mammals characteristic of each type are named. One diagram, several figures, and some tables illustrate the altitudinal and ecological affinities of the mammalian fauna and the physical factors that have influenced their dispersal throughout the state.

The greater part of the book is devoted to species accounts, which are rendered more meaningful by the introductory bio-ecological section that precedes them. In all, 144 subspecies of mammals are found to occur, or to have occurred in the recent past, within the limits of this Mexican state.

BRYAN P. GLASS

MAMMALS OF NORTHERN ALASKA *on the Arctic Slope. Univ. Kansas Mus. nat. Hist. misc. Pub. No. 8.*

By James W. Bee and E. Raymond Hall. University of Kansas Museum of Natural History, Lawrence. $4.00 (cloth); $1.00 (paper) 309 pp. + 5 pl.; text ill. 1956.

In the entire arctic slope area of Alaska only 41 species of mammals are known to occur, and only 29 of these are terrestrial. The details of the ecosystem of which each species is a part, and of the adaptations that permit each to survive, constitute a large part of this book. The problem of survival in the Arctic and the phenomenon of periodic fluctuation in numbers of individuals draw a generous share of the authors' attention.

Accounts of species occupy the major portion of the text. Three shrews, 1 hare, 8 rodents, and 4 ruminants are the mammalian prey available to 13 species of terrestrial carnivores. In addition, 6 cetaceans and 6 pinnipeds are known to inhabit the ocean bordering the Alaskan arctic shoreline. Each species is described in the classic way. The greatest contributions of the work are to be found, however, in the section entitled Remarks, for here are recorded virtually all of the observations made upon each of the species during the entire course of the study.

The plan of the book is somewhat the reverse of the usual practice; for the acknowledgments and various subjects of general consideration appear at the very end, rather than at the beginning. The section on geography and climate contains several very informative photographs of the arctic terrain.

BRYAN P. GLASS

RABBITS. *A Subject Bibliography.*

Compiled by Laura I. Makepeace. Bibliographical Center for Research, Denver Public Library, Denver. $2.00 (paper). xii + 81 pp. 1956.

This compilation is an attempt to produce a usable index to the enormous amount of literature on a group of animals that continues to gain importance in animal research. There are over 3400 separate entries, arranged alphabetically by subject. While not competent to judge the completeness of many of the categories, I nevertheless gain the impression that the subjects of physiology, pathology, ecology, and economics of rabbits and rabbit husbandry are well-reviewed. A taxonomist would be less pleased, upon noting that only Hall & Kelson, and Mearns, have been referred to. Even Nelson's review of the *Rabbits of North America* is not mentioned; and there is no reference whatsoever to any reviews of the rabbits of Europe, Asia, or Africa except indirectly through 11 citations of faunal lists from various parts of the world. In my own opinion, a more thorough treatment of the systematics of rabbits would greatly enhance the worth of this index. But even in its present form, it should prove invaluable to researchers using rabbits as experimental subjects.

BRYAN P. GLASS

NO ROOM FOR WILD ANIMALS.

By Bernhard Grzimek; translated by R. H. Stevens. W. W. Norton & Company, New York. $3.95. 271 pp. + 8 pl. 1957.

Bernhard Grzimek is Director of the Frankfurt Zoo. He is also, as the title of his book sugests, a champion for the cause of the many species of animals which currently face extinction. The book is a delightfully rambling account of a trip made by the author and his son to the Belgian Congo to collect specimens for the Frankfurt Zoo. Always extremely readable (in spite of the fact that it was translated from the German), the subject material ranges from actual accounts of Dr. Grzimek's experiences in collecting animals to the philosophy of "killing for sport"; from a "Short History of the Congo State" to an account of the discovery of the okapi and the Congo peacock. Included is a sur-

prising amount of information about the natural history of various inhabitants of Africa, especially elephants, hippos, okapis, rhinos, and pygmies. Much of this information is based on the author's own observations and is probably not generally known. *No Room for Wild Animals* is, if nothing else, a welcome relief from the usual sort of book on African animals.

M. A. BENDER

WATER. *The Yearbook of Agriculture, 1955.*

United States Department of Agriculture, Washington. $2.00. xiii + 751 pp.; ill. 1955.

Each year biologists, as well as farmers, have come to expect from the U. S. Department of Agriculture a comprehensive tome presenting both theoretical and highly practical information on some facet of agriculture, in an easily assimilable form. This particular volume continues the tradition, but inasmuch as it has the broadest scope, it is likely to be the least satisfying to any particular specialist. The editor's opening paragraph is a paragon of understatement as well as brevity: "There's a lot to be known about water."

As is only to be expected, the utilization and conservation of the farmer's basic need wins by far the greatest consideration. Where We Get Our Water, Water and Our Soil, Caring for Our Watersheds, Water for Irrigation, Drainage of Fields, and Pure Water for Farms and Cities are the titles of sections that concern themselves almost exclusively with these practical aspects.

The opening section, Our Need for Water, commences with a brief historical survey of five millenia of attempts to cope with the problem, and then moves with somewhat uneven pace to consider such matters as hydrogen bonding, animal requirements, transpiration, microbiological growth and development, and changing patterns of conservation requirements. Five sections deal respectively with the water requirements of forests, of crops, of ranges and pastures, of gardens, turf, and orchards, and of wild life. For the most part, the text is maintained at a conversationally informative level, but here and there appears an article or passage that will repay closer reading. Thornthwaite and Mather present the Water Budget and its Use in Irrigation with expected detail. Many will feel disappointed that a succeeding article in matching vein by Wadleigh —on Soil Moisture in Relation to Plant Growth—is only seven columns in length. Some will be lured, as the reviewer was, into interesting ecological reading by meeting unaccustomed terms such as "phreatophytes," if only to meet old friends like cottonwoods and tamarisk.

Perhaps the most disappointing section is the last. Entitled A Look to the Future, it stays at a rather mundane level for a world that is seething with an impulse to space travel. In summary, as far as biologists are concerned, this is a volume for browsing rather than for perusal.

DOUGLAS H. K. LEE

EVOLUTION

TRAITÉ DE PALÉONTOLOGIE. *Vol. V, Amphibiens, Reptiles, Oiseaux.*

Edited by Jean Piveteau. Masson & Cie., Paris. 12,000 fr. (paper); 12,800 fr. (cloth). viii + 1113 pp. 1955.

Since no extended account of fossil vertebrates has appeared since the days of the Zittel *Handbuch* of 1887–93, this volume, the first of four to be edited by Jean Piveteau which are to treat of fossil vertebrates, has been eagerly awaited. All the Amphibia and Aves and all Reptilia except the synapsids (reserved as an introduction to the mammals), are dealt with in this splendid work of over 1100 pages with nearly an equal number of illustrations. The illustrations include faithful reproductions of many of the most useful illustrations in classic and recent papers on the types concerned, as well as a number of new figures. Appended to the treatment of each group is a well-selected bibliography.

Ten per cent of the book consists of sections contributed by Swiss and Scandinavian workers; all the rest is from the pens of Professor Piveteau and his French colleagues and associates. No one country can, of course, furnish experts in every area of this vast field, and hence the quality of the various sections is not consistent. In some cases we have an authoritative treatment by a recognized leader in the study of a group, in others compilations which are less authoritative, although generally very well executed.

Much of the section on the Amphibia, constituting nearly a third of the volume, is the work of Lehman, who contributes an excellent general introduction to the class, good accounts of the rhachitomes and anthracosaurs (including seymouriamorphs), and a discussion of phyllospondyls. Jarvik furnishes a valuable summary of present knowledge of the most ancient amphibians, the ichthyostegids; Piveteau and Mlle. Dechaseaux jointly cover the trematosaurs and stereospondyls; Piveteau also treats the anurans; and Mlle. Dechaseaux discusses the lepospondyls and urodeles. For the older groups, the classification followed is generally that of the reviewer which, while admittedly provisional, is useful in the present stage of our knowledge. Lehman persistently considers various small, poorly ossified, and probably mainly larval labyrinthodonts to constitute an order Phyllospondyli. For the maintenance of this apparently mythical group, no reason

is given except for the report by Heyler that branchiosaurs have ventral vertebral elements. These look suspiciously like rhachitomous intercentra, and thus further confirm the artificial nature of the "order."

For the reptiles, Piveteau himself gives an introduction and covers in good fashion the cotylosaurs as well as several minor groups. Mlle. Dechaseaux treats the ichthyosaurs, Saint-Seine the sauropterygians and pterosaurs, and Peyer and Kuhn-Schnyder the placodonts and Triassic lizard-like forms. Kälin furnishes a thorough coverage of the crocodilians; and Hoffstetter, in addition to describing rhynchocephalians and thecodonts, gives a valuable account of fossil lizards and snakes—forms usually neglected in paleontological texts. Lapparent and Lavocat devote nearly 200 pages to the dinosaurs. Their treatment follows an orthodox pattern, except for a return to early practices of "lumping" stegosaurs and ankylosaurs in a common suborder —this on rather slight grounds. The least commendable section of the work is the account by Bergounioux of the turtles. His classification is one which I do not believe any modern student of the Chelonia would accept. It is of interest that he still maintains that an object which to all others appears to be a septarian nodule is a Permian turtle! The volume concludes with a chapter on fossil birds by Piveteau, assisted by Mlle. Dechaseaux.

Perfection, or near-perfection, is not to be expected in a work of this magnitude. The few criticisms I have made are not intended to show any lack of admiration for the notable accomplishment of Professor Piveteau and his collaborators. We shall look forward to the appearance of the remaining vertebrate volumes of the treatise with eagerness and confidence.

A. S. ROMER

TRIASSIC METOPOSAURID AMPHIBIANS. *Bull. Amer. Mus. nat. Hist., Vol. 110, Art. 6.*

By Edwin Harris Colbert and John Imbrie. American Museum of Natural History, New York. $1.00 (paper). Pp. 399–452 + 4 pl.; text ill. 1956.

The metoposaurs are large, degenerate Triassic end forms among the labyrinthodont amphibians. They had tiny limbs, flattened bodies, and flat heads with the eyes placed far forward in the long skull. They were widely distributed over the northern continents, but most of the remains are from North American deposits. In recent decades, most finds have been assigned to the genus *Buettneria* of Case, but a study of these forms has been hindered by a plethora of names—North American finds have been assigned to no less than 9 genera and 14 species, many of the latter founded on fragmentary material. Colbert and Imbrie have performed a useful service by reviewing the material and applying statistical methods to attempt a simplification of the taxonomic snarl. As a result, it seems clear that (apart from one problematical fragmentary specimen) all American metoposaurs can be assigned to a single genus, for which *Eupelor* Cope is the proper name, and that at most there are but three species, one from the eastern seaboard Triassic, one from Wyoming, and one from the southwestern states.

A. S. ROMER

THE BRACHYOPID LABYRINTHODONTS. *Bull. Brit. Mus. (nat. Hist.), Geol., Vol. 2, No. 8.*

By D. M. S. Watson. British Museum (Natural History), London. £ 1.0.0. (paper). Pp. 315–392 + 1 pl.; text ill. 1956.

Among the most important of early land vertebrates were the labyrinthodont amphibians—dominant in the Carboniferous and still prominent in the Permian and Triassic periods, despite the rise of the reptiles. A major landmark in their study was the publication by Watson in 1919 of a paper in which he pointed out a series of evolutionary trends within the group, and arranged the forms then known in three successive "grades" characteristic of the three periods during which the group flourished. In more recent decades a very large amount of new labyrinthodont material has been described, principally by workers in the United States, England, Sweden, and Russia; but no further attempt at a general treatment was made until the writer published a rather comprehensive review of the group in 1947. The data concerning known forms was there summarized, and the forms were arranged in a phyletic and systematic framework—not with the intent of "stabilizing" the situation, but rather to offer a point of departure for further advances in our comprehension of labyrinthodont evolution.

Watson's present paper is an important contribution to our knowledge of one segment of the group. In the Triassic period, an end line of labyrinthodonts is that of the brachyopids—relatively small forms with short, broad skulls. Watson has made a careful restudy of them and has attempted to determine their ancestry. In my 1947 review (see *Q.R.B.*, 23: 50. 1948), I provisionally adopted the view that the brachyopids had developed at a relatively late Permian date from a central stock of advanced rhachitomes. Watson, however, presents evidence suggestive of descent from a long line of short-faced ancestors, leading back through *Dvinosaurus* of the Russian late Permian to an early Permian form (*Eobrachyops*), contemporaneous with *Trimerorhachis* and distantly related to that genus. Valuable descriptions are given also of a number of short-faced Carboniferous labyrinthodonts; with one exception, however, these appear to show no close relationship to the later brachyopids.

A. S. ROMER

THE PERMIAN REPTILE *ARAEOSCELIS* RESTUDIED. *Bull. Mus. comp. Zool. Harv., Vol. 113, No. 5.*

By Peter Paul Vaughn. Museum of Comparative Zoology at Harvard College, Cambridge. $1.50 (paper). ii + pp. 305–467 + 2 pl.; text ill. 1955.

The Permian reptile, *Araeoscelis*, has until now been known largely from the original description by Williston in 1910, and from other descriptions, almost as old, by Case and by Broom. In this very important contribution to our knowledge of reptilian evolution, Peter Paul Vaughn presents a new and detailed study of *Araeoscelis* that is concerned not only with detailed descriptions of the osteology of the reptile, but also with a long and well-considered evaluation of the position of *Araeoscelis* in reptilian classification, and of its bearing upon early reptilian history. For various reasons this paper is of extraordinary significance to students interested in the evolution of reptiles and the relationships between them.

Vaughn's description of the osteology of *Araeoscelis* gives us a picture of this reptile that is considerably modified from the concepts hitherto held, based largely upon the work of Williston, Case, and Broom. Briefly, he shows that *Araeoscelis* is essentially a primitive reptile, as indicated by the basically primitive pattern of the skull bones and by various characters of the postcranial skeleton, in which there is an overlay of certain "habitus" features that mark this animal as an "adaptive lizard" of Permian age. For instance, within the generalized arrangement of the bones that constitute the posterior part of the skull there is inserted, as it were, an upper temporal opening—an adaptation allowing for increased efficiency of the temporal muscles. The temporal fenestrae, long thought by many students to be of considerable importance in determining reptilian relationships, are considered by Vaughn to be of secondary value in this regard. Thus he sees the upper temporal opening in *Araeoscelis* as an independently derived feature, perhaps having little or nothing in common with the similarly placed opening in the synaptosaurian reptiles.

Continuing, he shows that in the postcranial skeleton the slender limbs and feet, the elongated vertebrae, and the generally light build are largely functions of absolute size and the special adaptations of *Araeoscelis* as a "lizard type." He demonstrates that the pectoral girdle is not at all the strange structure described by Williston, but rather a characteristic reptilian girdle of primitive type, with two large coracoid elements, a "screw-shaped" glenoid cavity, a long-stemmed interclavicle, and an ossified sternum. The pelvis is of the primitive reptilian type, similar to the pelvis in the ophiacodontid pelycosaurs. As already remarked, the limbs are slender. The manus shows some elongation. The pes is characterized by large proximal elements, with a firm joint between the tibia and the astragalus. The fifth digit is quite divergent, an independent development that strengthens Vaughn's analogy of *Araeoscelis* as a "lizard-like" reptile. The ribs approach a holocephalous condition through the diminution of the capitulum.

Important as many of these osteological features are, Vaughn considers none of them to be completely definitive in determining the relationships of *Araeoscelis*. Some features, as he shows, are primitive characters that relate *Araeoscelis* with the ancestral cotylosaurs, while others are habitus features that tend to mask the affinities of the genus. He therefore gives particular importance to the middle ear as a clue to the relationships of this reptile; indeed a considerable portion of his paper is devoted to consideration of the otic region. Quite a number of years ago, Goodrich developed the idea that there was a primary division of reptiles from a basic anapsid stock. Those two reptilian branches, according to Goodrich, are the Sauropsida, a line that eventually led to the birds, and the Theropsida, a line that eventually led to the mammals. Goodrich based his concept primarily upon the structure of the heart and secondarily upon the structure of the fifth metatarsal. Of course, the anatomy of the heart is of no value in a consideration of fossil materials; and, as Vaughn shows, the structure of the fifth metatarsal is not always a consistent criterion of basic relationships. Vaughn analyzes the otic region as a clue to sauropsid and theropsid relationships according to a theory developed some years ago by Watson, and, of course, giving consideration to the work of Parrington, Westoll, Romer, and Olson on this problem as well. It was Watson's contention that the primary division of the reptiles into sauropsid and theropsid lines might be recognized at an early stage in their history by the development, or lack of development, of an otic notch within the cotylosaurs. Watson felt that those cotylosaurs with a prominent otic notch, the diadectomorphs, led to the sauropsids, in which there was a well-developed tympanic membrane from which vibrations were transmitted to the internal ear by an elongated stapedial complex. In the captorhinomorph cotylosaurs, on the other hand, there is no such otic notch; and Watson stipulated that the synapsids, derived from these cotylosaurs, went through a stage in their development during which the tympanic membrane was lost and hearing was by bone conduction. In these reptiles the stapes is generally a heavy bone. Thus, according to Watson's theory, the tympanic membrane of the mammals is a new feature, not homologous with the tympanic membrane in the sauropsid reptiles and the birds. Subsequently Westoll propounded a modification of Watson's theory, whereby a portion of the mammalian tympanic membrane might be considered as homologous with the labyrinthodont membrane. According to this idea there was never a complete loss of hearing by air-borne sounds in the theropsid reptiles. Vaughn attempts a reconciliation of the two theses. He sees, in the evolution of sauropsids and theropsids, a difference of emphasis in different portions of the original fish

hyomandibular, which eventually became the tetrapod stapes. The evolution of the reptilian mechanism to hear air-borne sounds followed two successful and divergent lines of development. Consequently, according to Vaughn, "the basic split of the reptilian stock may be looked upon as true dichotomy and need not be considered as diphyly."

Vaughn makes detailed comparisons of *Araeoscelis* with all of the genera of reptiles that have been classified as protorosaurs. He shows that the order Protorosauria is in truth a taxonomic waste basket, containing various forms that have little in common with each other. As a result of his study, he removes *Araeoscelis* from the protorosaurs and establishes it as representative of an infraorder Araeoscelidia of the captorhinomorph division of the cotylosaurs. Consequently, *Araeoscelis* is placed among the theropsid reptiles and is regarded as having nothing to do with the plesiosaurs, which Vaughn considers as of probable sauropsid relationships. In short, *Araeoscelis* becomes an anapsid with a fenestrated skull.

Whether or not one agrees with all of Vaughn's conclusions, it can readily be said that he has published a monograph of unusual significance, a paper that will be a primary source of reference to students of reptilian evolution. The one major criticism that might be made of his contribution is that it lacks figures in the latter portion of the work. Comparative figures and diagrams would help greatly in following his discussions of the evolution of the ear in reptiles and of the comparisons between *Araeoscelis* and other reptiles. As it is, the reader who lacks a phenomenal memory for details is forced to dig out various publications to refresh his recollections, and this is a nuisance.

E. H. COLBERT

GENETICS AND CYTOLOGY

TRAITÉ DE GÉNÉTIQUE. *Tome II. La Génétique des Populations.*

By Ph. L'Heritier. Presses Universitaires de France, Paris. 900 fr. 273 pp.; ill. 1954.

La Génétique des Populations is the second of a series of three works by L'Heritier. In the present volume he discusses the genetic structure of bisexual populations and the changes going on in them. In the first chapter, entitled Various Systems of Crossing and the Genetic Structure of Populations, the author stresses the immense amount of genetic variability found in natural populations. This variability may be expressed as visible polymorphism, as in man and *Cepaea nemoralis*, or as "cryptopolymorphism," also in man and in wild *Drosophila* populations which are heterozygous for many recessive mutants. Several species of *Drosophila* and a *Sciara* species are polymorphic for various types of inversions. The genetic diversity found in most wild populations, subject to changes due to natural selection, mutation, migration, and chance, form the basis for evolutionary development. The author points out that a system of random breeding is only approximately achieved in nature, as in human populations of large cities and in oysters (with mobile gametes). In the simple case in which two autosomal alleles have the same frequency in the two sexes, a single generation of random mating results in a population at equilibrium with a frequency of p^2: 2 pq: q^2 for the three respective genotypes, according to the Hardy-Weinberg Law. In the more complicated cases in which the alleles do not occur with the same frequency in the two sexes, or where the alleles in question are sex-linked, random breeding rapidly produces a stable equilibrium. Linkage slows up a mixing of genes in a panmictic population. Inbreeding regularly occurs in many plants, often in birds, bees, galls, and even as much as 30% first-cousin marriage is found in certain human populations. Position inbreeding—a tendency to choose a mate from a near geographical area—has been described in *Cepaea nemoralis* by LaMotte. This type of mating system leads to heterogeneity within the structure of a large population, which becomes broken into semi-isolated subgroups. Within each subgroup the gametic coefficient of correlation approaches unity as the alleles in the subgroups become homozygous. Homogamy (a tendency of like phenotypes to mate) can modify the genetic structure of a genetic population, leading toward homozygosity of subgroups if this type of breeding system is sufficiently used.

The second chapter is devoted to a review of the works of Dahlberg, Fisher, Haldane, Teissier, and Wright on the respective roles of selection, mutation, migration, and chance in causing variations in gene frequency in wild populations. The author begins with the simplest case, viz., selection on the haploid phase (as in plants) of a large population, and with constant coefficients of selection. The favored allele then quickly invades all the loci if its selective advantage is much above 1. Still assuming a large population, selection in favor of one of a pair of autosomal alleles among zygotes is complicated by the fact that selection can work at any time in the life cycle between fertilized egg and adult. Further, selection can operate on adult stages by its differential influence on fertility. The author considers the simpler cases in which the selective advantage of the genotype homozygous for the one or the other allele is superior to that of the heterozygote. Here, although the favored allele rapidly invades all available loci, the speed of replacement is always weakest when p or q, the respective frequencies of the two alleles, are in the neighborhood of zero. Hence, when the frequency of a disadvantageous gene becomes low, selection thenceforth works against it very slowly. A sex-linked lethal gene is eliminated much faster than

an autosomal lethal. The author later develops the more general case where the selective coefficients of three genotypes, a/a, a'/a, a'/a' are complex functions of other genes in the population. The mean selective value of a population now becomes a function not of the frequency of a single locus, but of all genic frequencies at all loci. The variations of this complex function may be represented by a hypersurface. Selection leads a population to occupy a peak or elevated spot on this hypersurface of peaks and valleys. Gene mutation, always a rare event, slowly modifies the genetic composition of a population. The author points out that the use of atomic energy in industrial and military goals may increase enormously the spontaneous mutation rate in humans. He might well also have mentioned that the present-day wide use of radiation in medicine undoubtedly contributes to an increase of the spontaneous mutation rate. Migration has the same effect as mutation in transforming populations. In the absence of selection, if two genes mutate to one another with a definite frequency, the population approaches an equilibrium with respect to the two alleles very slowly. The equilibrium point of genic frequencies of a pair of alleles is determined and curves are pictured for several cases in which selection interacts with mutation.

If the size of a population is limited, the proportions of an allele, a, among the gametes will not exactly correspond to "p", the frequency of a in the parent population. This error causes a disorganized movement from the point of equilibrium of a, called fortuitous drift. Drift can cause the loss of one or the other of two alleles, in the absence both of mutation and selection if the population size is small. Drift, together with a relatively weak change in mutation rate, can bring about enormous modifications in genic frequencies. In *Cepaea nemoralis*, LaMotte showed that the genic frequencies among small-sized colonies are more variable than among colonies of enormous size, doubtless owing to genetic drift.

The author devotes the last chapter to a consideration of the Neo-Darwinist interpretation of the mechanism of evolution. Since it is not individuals but populations which have evolved, a theory of the mechanics of evolution belongs to the domain of the genetics of populations. The author believes it justifiable to extrapolate a genetic theory of evolution into a theory extending over geologic time spans. He disagrees with Simpson's concept of "species without dimensions" as applied to sympatric species biologically isolated from one another. Every population, says the author, has geographical dimensions which, with position inbreeding, may lead to a splitting of the population. The author believes that cytoplasmic heredity must be incorporated into the classical Neo-Darwinist theory. He points out that the basic difference which has arisen between animals and plants is one of plastids carried in the cytoplasm. The author thinks that even should evolution proceed sometimes by big steps as postulated by Goldschmidt, this method is not necessarily universal.

The reader interested in experimental work on speciation will find this volume stimulating and helpful. For example, in studying seasonal fluctuations of wild *Drosophila* species, I myself found these populations existing in very small numbers for a number of months of the year. In these species, fortuitous drift must have an important influence on genic frequencies. This work on the genetics of populations is valuable also to the genetics teacher, although it is not designed as a textbook, as is Li's book on the same subject. The organization of the present volume is compact and well coordinated. The book is unfortunately paper-bound and has uncut pages.

SARAH B. PIPKIN

CAT GENETICS.

By A. C. Jude. All-Pets Books, Fond du Lac. $3.50. x + 126 pp. + 21 pl.; text ill. 1955.

This book is primarily for the cat fancier, and includes a great deal more information about the various breeds than the title would indicate. Only about one-fourth of the book deals specifically with genetic mutations in the cat. The author felt it necessary to include background material on general biology, variation, and evolution, as well as basic genetic theory. This is unfortunate, for he has often oversimplified to the point of misconception and error. He says, for example, that ". . . in order to prevent their living matter from being flowed away, amoeba [sic] are protected by walls of skin"; and, "This is the nucleus, the primitive forerunner of the brain." Again, the "sperm. . . on contact with the ovum brings life to it and commences the life of a new offspring."

The portions of the book designed to supply adequate knowledge of Mendelian mechanisms to the neophyte probably fall short of their goal. Major attention in considering the genetics of cats is given to hair length and coat color, with some information about polydactyly and tail length. Most of the information in the chapters on habit, the glands, eyes, ears, and diseases, while of value, has little to do with genetics.

The book is not well written—indeed, the entire manuscript should have been carefully edited. Yet with all its shortcomings, the book may deserve a place on the bookshelf of the breeder of fancy cats, since some of the information it contains is not easily accessible. The text is accompanied by an excellent series of photographs, 22 plates in all, which illustrate the most widely known breeds, as well as the products of some unusual crosses.

FRANK C. ERK

PLANT PHYSIOLOGY

PLANTS IN ACTION. *A Laboratory Manual of Plant Physiology.*

By Leonard Machlis and John G. Torrey, illustrated by Evan Gillespie. W. H. Freeman & Company, San Francisco. $3.75 (paper). vi + 282 pp.; ill. 1956.

A number of interesting features of *Plants in Action* make it a valuable manual of plant physiology. In the first place, the students will find themselves immediately concerned with handling plants—growing them, measuring them, weighing them, comparing them. Throughout the book the student becomes familiar with a wide variety of plants and plant tissues. This promotes high student interest in physiological problems. Secondly, the experiments emphasize those aspects of plant physiology that lend themselves to quantitative techniques. Methods of measuring, weighing, colorimetry, spectroscopy, and chromatography are introduced. Thirdly, the experiments are slanted toward the concept that biochemistry and metabolism at the cellular level are the unifying principles of plant physiology. Finally, the experiments are tied together with explanatory text that points up where the experiments stand in relation to the broad problems of plant physiology.

The experiments are divided into four major divisions: Plant Development, Mineral Nutrition, Water Relations, and Cellular Metabolism. In all, 57 experiments are involved. Both the textual material and the experimental sections are well illustrated, and directions are complete. In addition there are three appendices. The first introduces some of the basic concepts of light and photochemical reactions. The second describes the determination of the standard deviation and the standard error. The third appendix gives a time-table for supplying the laboratory with plant material (sources of plant material as well as a planting schedule are included). A list of equipment and reagents needed for each experiment is also included. Tear-out report sheets are provided for the experiments. This laboratory manual can be highly recommended.

G. R. NOGGLE

ECONOMIC BOTANY

AN INTRODUCTION TO THE BOTANY OF TROPICAL CROPS. *By Leslie S. Cobley. Longmans, Green & Company, London, New York, and Toronto.* $7.25. xv + 357 pp. + 82 pl.; ill. 1956.

The tropics have always been a fascinating area botanically; and today, when the increasing ease of communication and transport and the demands of the rapidly increasing world population have focused attention on them as a source of food and raw materials, any authoritative addition to the literature is welcome.

The present book, unlike most of its predecessors, stresses the botanical aspects of tropical crops. This in itself makes the work a most valuable contribution, for in the past much of the information now brought together in its pages has been available only in widely scattered sources. Sufficient data are also given regarding distribution, areas of cultivation, and uses so that a fairly complete picture of each species is provided.

The author admits that the treatment is somewhat superficial because of the great number and variety of tropical plants. Moreover, certain groups are omitted, such as gums and resins, forage plants, and plants with possibilities for future development. Even so, 150 species or more are discussed under the general headings of Cereal Crops; Sugar Cane; Vegetable Fibres; Oil Seeds; Leguminous Crops; Starch Storage Crops; Spices; Beverages and Drug Plants; Cultivated Fruits; Vegetable Crops; Rubber; and Essential Oil Crops. There is a special list of references at the end of each chapter. The book is well illustrated with plates and line drawings. There is a List of Books for Further Reading and General Reference, an index of "botanical" names, and a general index.

Some of the omissions are surprising. One looks in vain for a discussion of the Brazilian oil palms, cola, or the cashew; and very little space is devoted to jute, an outstanding tropical crop. Moreover, in future editions, it might be preferable to include a greater variety of tropical fruits and drug plants, rather than flax, soybean, sunflower, peanut, common bean, alfalfa, and tomato, which are equally, or even more, characteristic of the warmer temperate regions. These are minor criticisms, however, and do not detract from the value of the book as a textbook and general reference work.

ALBERT F. HILL

GRASSLANDS OF THE GREAT PLAINS. *Their Nature and Use.*

By J. E. Weaver and F. W. Albertson, with special chapters by B. W. Allred and Arnold Heerwagen. Johnsen Publishing Company, Lincoln. $6.50. x + 395 pp.; ill. 1956.

Since so many of our areas of natural vegetation are undergoing profound changes at the hands of man and other agencies, it is essential for the benefit of future generations that some record be made of the original plant communities and their environmental relations. Such a survey was made for the prairies in *North American Prairie*, by J. E. Weaver. Now comes a companion volume, *Grasslands of the Great Plains*, by J. E. Weaver and F. W. Albertson, two scientists who have devoted the greater part of a lifetime to an intimate study of this area.

The Great Plains, one of the world's largest expanses of grassland, extend from southern Texas to central Saskatchewan and Alberta. They are characterized by the mixed prairie type of vegetation, consisting primarily of perennial short and mid grasses and a large number of forbs (non-grasslike plants).

The various plant communities that comprise this area are here described in detail, both as they appear above ground and deep into the soil as well. Their nature, composition, significance, climatic and edaphic relations, and uses are all considered. The most important contributions that have made possible this accurate description and interpretation are reviewed, from the coming of the white man to the present day.

The deleterious effects of agriculture—over-grazing, drought, and the resulting dust storms—are given special consideration. Even more important, the book points out how the plant cover of flourishing grassland, so necessary for building and protecting the soil, may be restored.

A general account of the mixed prairie and the most important species is followed by a series of regional treatments. Kansas, where the mixed prairie has been studied over a very long period, both before and after the drought, is considered in detail as the following chapter headings indicate: Plant Communities in Western Kansas; Beginning of the Great Drought; Changes in Vegetation in Drought; Vegetation at the End of Drought; A Regional Survey; Recovery of Vegetation; and Ten Good Years.

Two chapters are devoted to Nebraska and one each to Colorado, Oklahoma, Texas (contributed by B. W. Allred), New Mexico (contributed by Arnold Heerwagen), the Northern Great Plains (chiefly North Dakota), South Dakota, Montana, and Wyoming, and the Canadian mixed prairie. One chapter deals with the forbs, and another with Plains Plants Underground.

A list of species with both common and scientific names, an extensive bibliography, and an index are also supplied. The book is well illustrated and the typography is excellent.

Grasslands of the Great Plains will be welcomed by all botanists, whether or not they are ecologists. For students of range management, range technicians, conservationists, and ranchers, indeed any and all who are interested in the efficient use of the midwestern native grasses and other forage plants, it will be well-nigh indispensable.

ALBERT F. HILL

GRASSLAND FARMING.

By George H. Serviss and Gilbert H. Ahlgren. John Wiley & Sons, New York; Chapman & Hall, London. $2.96. viii + 146 pp.; ill. 1955.

Recognizing the importance of grassland farming in our national economy, and also the fact that present-day practice requires much technical knowledge, management ability, and operative skill, the authors have prepared this little book for students in high schools and junior colleges and for farm operators and managers.

Each of the chapters is devoted to some actual farm operation and presents the most important results of research and the principles and practices of production and management. They include: Growing Grassland Crops, Using Forage in Livestock Feeding, Growing Forage for Profit, Selecting Legumes, Selecting Grasses, Choosing Seed and Establishing Seedlings, Adding Lime and Fertilizer, Managing Pastures, Managing Hay Crops, Preserving Forage, Conservation Cropping, and Equipping the Grassland Farm. A selection of suggested readings and a series of Questions and Activities are given for each chapter.

In an appendix, there are presented in tabular form a Green Pasture Score Card, a List of Grasses and Legumes with Seed per Pound and Seeding Rates per acre, Standard Weights per Bushel, Weights and Measures, Some Popular Grass and Legume Mixtures, Capacity of Silos, and Soil Reaction Preferences of Forage Crops.

ALBERT F. HILL

FORAGE CROPS. *Second Edition.*

By Gilbert H. Ahlgren. McGraw-Hill Book Company, New York, Toronto, and London. $7.00. vii + 536 pp.; ill. 1956.

The second edition of this valuable book has been carefully revised, and much new material has been added, incorporating the results of recent investigations and the suggestions of the many users of the first edition (*Q.R.B.*, 26: 65. 1951). New chapters on pasture and range management are included.

In its 39 short chapters, the book presents a concise, but entirely adequate account of the characteristics and adaptations of the most important legumes and grasses; the agricultural practices common to all forage crops, including hay, pasture, silage, and seed production; and diseases, insect pests, and other problems. The book is profusely illustrated with drawings, photographs, charts, maps, and tables. Although written primarily for students, the new edition continues to be an excellent reference work for anyone interested in agriculture in general.

ALBERT F. HILL

CROP PROTECTION.

By G. J. Rose. Philosophical Library, New York. $10.00. xxii + 223 pp. + 63 pl.; text ill. 1955.

When primitive man first became an agriculturist he unconsciously upset the balance of nature and created optimum conditions for weeds, insect pests, and plant diseases. Ever since, the farmer has been faced with the problem of protecting his crops against these enemies by using some type of control measures. Such measures may be ecological, cultural, biological, or chemical in nature, the latter constituting probably the most effective method. In recent years scientists have greatly increased our knowledge of the science of crop protection. Rose's book is an attempt to integrate these scientific achievements and to make them intelligible to practical farmers. It is not only a guide to the protection of crops from seed to stored product, but an aid to the planning of a control program as well.

Section I is devoted to a general consideration of cultural control, the types of available materials—dusts, baits, smokes, fumigants, emulsions, suspensions, etc., and the choice of materials. Section II discusses the various chemicals utilized as weed killers, insecticides, fungicides, or rodenticides. Section III is concerned with application machinery—including dusting systems, spraying systems, injection systems—and the choice, operation, and maintenance of the equipment. Section IV deals with the protection of stored products.

Specific treatments for some forty crops are given in a summary of control measures. There is an appendix devoted to conversion tables and an index.

ALBERT F. HILL

SOIL FERTILITY AND FERTILIZERS. *By Samuel L. Tisdale and Werner L. Nelson. The Macmillan Company, New York.* $7.75. xxii + 430 pp.; ill. 1956.

This book is written for students and others who have had at least the basic course in soil science. It is a clear and concise treatment of the history of soil fertility and fertilizers, of plant requirements for nutrients, and of methods and techniques used in supplying plant nutrients to soils and crops.

In the first part of the book the authors discuss the factors affecting plant growth; the elements required in plant nutrition; and the forms and reactions of soil nitrogen, phosphorus, potassium, magnesium, and sodium. Secondary and trace elements are also considered.

The manufacture of mixed fertilizers is fully explained in relation to kinds, analysis, physical condition, dry and liquid and other properties. The composition, handling, and value of manure; soil acidity; liming materials; and the use of lime in agriculture are discussed.

In later chapters the problems of evaluating fertility needs for crop production, methods of applying fertilizers, and cropping systems and soil management are given. The book concludes with information on the economics of using lime and fertilizer in growing crops, and gives some background as to what kind of approach to use in solving new soil fertility problems as they arise.

Style and clarity are excellent. So also are the well-chosen illustrations, graphs, and tables that give added emphasis to the discussion. This book should be a valuable teaching aid for advanced courses in the subject and a good reference work for those interested in soil fertility and fertilizers.

GILBERT H. AHLGREN

ELEMENTS OF SOIL CONSERVATION. *Second Edition. By Hugh Hammond Bennett. McGraw-Hill Book Company, New York, Toronto, and London.* $3.96. x + 358 pp.; ill. 1955.

The problems of soil and water wastage, from historical and present-day points of view, are ably discussed here by a leading authority on the subject. Thereafter, the book deals in some detail with improved methods of preventing soil erosion and water losses. Everyone interested in these subjects will find this a valuable publication, whether for teaching or as a reference book.

In the forepart of the book the problem of erosion, including its extent and its effect on our community and national life, is discussed. The causes of erosion and factors that accelerate them are reviewed, and an insight into the formation of the National Soil Conservation Program is given.

The author describes the methods of initiating conservation planning and discusses vegetation, contouring, terracing, water spreading, and other means of saving soil and water. The relation of wildlife to soil conservation, the use of farm ponds for storing water, drainage and irrigation in soil conservation, stubble-mulch farming, and the use of trees and shrubs in conservation are considered. The book ends with a discussion of the importance of upstream flood control.

The author's critically-chosen illustrations add greatly to an understanding of the text, which is written in a clear, concise, and authoritative style. This book is highly recommended as a ready means of gaining a broad appreciation of our soil and water problems.

GILBERT H. AHLGREN

GENERAL AND SYSTEMATIC ZOOLOGY

FORTSCHRITTE DER ZOOLOGIE. *Neue Folge, Band 10. Im Auftrage der Deutschen Zoologischen Gesellschaft unter Mitarbeit von Fachgenossen.*

Edited by Max Hartmann. Gustav Fischer Verlag, Stuttgart. DM. 55. iv + 598 pp.; ill. 1956.

The tenth volume of the *Forschritte der Zoologie* (new series), edited by Max Hartmann, contains the following reviews, all in German: Morphology and Developmental History of Protozoa, by K. G. Grell (26 pages of text, 5 pages of bibliography); Systematics and Phylogeny of Vertebrates, by Klaus Günther (198 pages of text, 58 pages of bibliography); Hormones, by H. Giersberg (18 pages of text, 8 pages of bibliography); Muscle Physiology: the Effect of Adenosine Triphosphate on Contractile Proteins and the Contraction of Muscle and Cells, by H. H. Weber (68 pages of text, 7½ pages of bibliography); the Central Nervous System, by E. von Holst (8 pages of text, 1 page of bibliography); Diplogenetic Sex Determination, by L. Wiese (46 pages of text, 2 pages of bibliography); Phenotypic Sex Differentiation, by C. Hauenschild (9½ pages of text); Fertilization and Gamones, by C. Hauenschild (7 pages of text, 2 pages of bibliography, including also references on phenotypic sex differentiation); Developmental Physiology of Vertebrates, by C. von Woellwarth (86 pages, 16 pages of bibliography); and Physics and Chemistry of the Cell, by H. Friedrich-Freksa (31 pages, 5 pages of bibliography).

That the intent of the various articles differs is clear from their disparity in length. The very short article on the central nervous system deals exclusively with muscle spindles and proprioceptors. The long article on systematics, which is almost a book in itself, discusses not only specific taxonomic details but also broad general problems: theory and method, the species concept, transspecific evolution, etc. Most of the articles are thoughtfully presented and useful. As embryologist, the reviewer would like to direct a special compliment to von Woellwarth. His review of vertebrate developmental physiology, which confines itself principally to a discussion of experimental morphology of the amphibian, is a penetratingly critical and constructive study, both wide and intensive, and deserves to be widely read.

JANE OPPENHEIMER

KINSHIPS OF ANIMALS AND MAN. *A Textbook of Animal Biology.*

By Ann H. Morgan. McGraw-Hill Book Company, New York, Toronto, and London. $6.75. viii + 839 pp.; ill. 1955.

The title of this book is a bit misleading because of the interpretation most persons will usually make of it. It is not a discussion of evolution or taxonomic ancestry, but, as the subtitle indicates, a textbook of animal biology. It is quite comprehensive and detailed; for these reasons, it would be a more satisfactory textbook in a full year course than in a single semester course.

The book is well written and well illustrated. The more modern concepts of most topics are presented. The text has been well edited; no abundance of gross or minor errors were detected. The organization and objective in the textual arrangement are clear to a zoologist, but I am not sure that they will be clear to the beginning student. A tremendous amount of detailed subject matter is included, but these details tend to be scattered and one wonders, will the beginning student become lost in the forest because of the many, many trees? Only classroom use can answer this question.

This, yet another, textbook in general zoology includes the usual subject matter in much the same sequence as that found in a multitude of others. It is unique, however, in that the theme throughout the book is that "relationships are persistently evident in our world and universe." There are relationships of animals to one another; of animals to plants; of animals to water, sun, earth, seasons, matter, and energy. There are also relationships between tissues, organs, and parts inside and outside of the individual.

The text starts with an introduction to the basic relationships of the universe and life: matter, energy, living material, and cells. Plants are then considered as sources of energy for all living things. And, unique for a zoology textbook, there is a comprehensive chapter on basic plant anatomy and physiology. Two sections on Animals and Environments and on Animal Relationships follow; these are basic ecology. Then comes a survey of the internal environment of an organism; this is a résumé of human physiology. The next chapter deals with the new individual, its development and heredity. The last half of the 839-page text is entitled Evolution of Animals and Evolution and Conservation. The first portion is a survey of the animal kingdom with emphasis on phylogenetic relationships.

The discussion on conservation is very brief and leaves much to be desired. An appendix of reference materials and an adequate index are provided, but there is no glossary.

ROY W. JONES

PROCEDURE IN TAXONOMY, *Including a Reprint in Translation of the Règles Internationales de la Nomenclature Zoölogique (International Code of Zoological Nomenclature) with Titles and Notes on the Opinions Rendered to the Present Date (1907 to 1956) Completely Indexed. Third Edition.*

By Edward T. Schenk and John H. McMasters, revised by A. Myra Keen and Simeon William Muller.

Stanford University Press, Stanford. $3.50. vii + 119 pp. 1956.

In reviewing the first edition, R. A. Wortham wrote in 1936, "With the application of the rules laid down in this book, in the course of a few years the study of taxonomy will be a pleasure instead of the 'bad headache' of today." We are forced to admit, some twenty years later, that there are still a great many headaches in the taxonomy business, arising mainly from nomenclatural problems rather than biological ones. Theoretically, nomenclatural problems could be solved by following the "rules," but the International Congress of Zoology has not been very helpful in this respect, altering the rules in 1948 and again in 1953. This new edition has been rewritten in part with the Copenhagen Decisions of 1953 in mind. The list of titles of *Opinions* issued by the International Commission has also been brought up to date; and the authors have included the titles of the two new series of directives, the *Declarations* and the *Directions*, initiated recently by the Commission. Declaration 9 of the Commission expresses the desirability of including zoological nomenclature in university courses in general and systematic zoology. This small, compact volume could well serve as an introduction, to be followed by *Methods and Principles of Systematic Zoology*, written by Mayr, Linsley, and Usinger. For the student, the sections dealing with systematic categories, types, specific names, and Latin terms and abbreviations will be especially helpful; they are well written and not unduly technical. For the taxonomist, the complete and highly practical index to the Rules and Opinions should help reduce the need for aspirin.

MARSHALL R. WHEELER

PROTOZOOLOGIE.

By Karl G. Grell. Springer Verlag, Berlin, Göttingen, and Heidelberg. DM 59. viii + 284 pp.; ill. 1956.

In a charming, concentrated, and competent fashion, Grell brings one up to date on developments in the field of protozoology, with primary emphasis on the nuclear conditions and life history of the Protozoa. His small volume, lavishly and tastefully illustrated, presents selected material bearing on many of the classical protozoan problems and their relation to metazoan cytology. This book should be particularly welcome at a time when major concentration appears to be placed on nutritional, biochemical, genetic, and parasitological aspects of the investigation of the Protozoa. To be sure, the appeal of this book reflects the scholarship and experience of its author, who has had a first-hand research familiarity with a wide variety of Protozoa—ciliates, Suctoria, Foraminifera, Coccidia, and Radiolaria.

As the title indicates, the treatment of the subject is comprehensive, but it is not exhaustive. Throughout, the thread of continuity is maintained by tracing the relationships of chromosomal and nuclear history to life cycles and reproductive and sexual processes in all the groups of the Protozoa. The bearing of newer discoveries on changes in the understanding of basic cytological problems is consistently pursued, so that the approach is fresh and stimulating. Appropriately, L. R. Cleveland's important observations on chromosome structure and behavior in woodroach flagellates are given extensive treatment, and much of the recent work on *Paramecium* is thoroughly covered. The newer interpretation of foraminiferan life cycles, largely the result of Le Calvez' work, is analyzed and presented in detail.

The first part of the book is devoted to morphology: cytoplasmic structures, the nucleus, mitosis, and meiosis. Then comes the main section on reproduction in its manifold aspects. This material occupies about 160 pages. Following this are brief chapters on movement, behavior, nutrition, parasitism, and symbiosis, totalling 24 pages. The next 80 pages are devoted to a systematic survey of the Protozoa. This section is necessarily abbreviated, but it does deal with all the major groups of organisms which Grell considers to be Protozoa. Illustrations of the taxonomic and morphological features of representative organisms, as well as diagrams and charts of life histories, are given in this section.

Some of the taxonomic decisions are debatable and will be accepted reluctantly by American protozoologists. The Opalinida are removed from the Protociliata and are considered to be an order of the Flagellata. The Hypermastigidae are transferred to the order Polymastigina. Without much ceremony, the entire group of the Cnidosporidia is deleted from the Protozoa on the basis of a differentiation among the somatic cells and nuclei. The Coccidia are divided into two suborders, the Eucoccidia and Schizococcidia, on what appears to be insufficient evidence. The transfer of the Haemosporidia from a separate order to a family Haemosporidae of the Coccidia seems sensible following the discovery of the exo-erythrocytic stages of various species of *Plasmodium*.

The author and publisher are to be congratulated for their numerous and excellent illustrations, averaging more than one per page. Well-chosen and well-reproduced photographs have been generously used. Many diagrams and charts have been redrawn or freshly designed in a clear and attractive style. A bibliography of general reference works and cited papers (380 titles) concludes the book. An interesting innovation is the inclusion of a list of films dealing with the Protozoa.

The author writes simply and clearly. He has integrated much detailed material and has organized it into easily handled form. All in all, he has made a very useful contribution to modern protozoology.

WILLIAM F. DILLER

THE AMERICAN ARBACIA AND OTHER SEA URCHINS. *By Ethel Browne Harvey. Princeton University Press, Princeton.* $6.00. xxiv + 298 pp. + 16 pl.; text ill. 1956.

In a way it is surprising to realize what physiologists and embryologists can think of doing to one unfortunate animal (or its eggs), but all arbaciologists will welcome this book as an indispensable guide to the literature and a summary of what has been done in the field. The book is well unified by means of chapters on general aspects of sea urchins, with special reference to *Arbacia*, on "normal development," and on the properties of centrifuged eggs. A concise abstract of experimental work culminates in a 50-page bibliography. Sixteen fine plates, principally of various types of development of the egg, complete the volume.

Between 1933 and 1950, some 292,000 *Arbacia* were used at Woods Hole. Nonetheless we read in the brief chapter on natural history that "no data have been found for geotropism in *Arbacia*" and the "cause of the decreasing quantities of *Arbacia* around Woods Hole is not known." While it is conceded that the decline may be due in part to the requirements of the experimenters (some times at the rate of several hundred a day), it is unfortunate that so little is known of the natural history of this animal. What, for example, is the fate of the undersized specimens returned to the sea? The future of work on *Arbacia* may be dependent upon the answer to this and similar questions, as well as upon a less extravagant use of material by the individual experimenter. Such remarks are not intended to detract from the quality of an excellent book. They are inspired by the three blank sheets at the end, obviously intended for further additions to the bibliography by owners of the book.

JOEL W. HEDGPETH

THE RECENT GENERA OF THE CARIDEAN AND STENOPODIDEAN SHRIMPS (CLASS CRUSTACEA, ORDER DECAPODA, SUPERSECTION NATANTIA) WITH KEYS FOR THEIR DETERMINATION. *Zool. Verh. Rijksmus. nat. Hist., Leiden, No. 26.*

By L. B. Holthuis. E. J. Brill, Leiden; [*National Research Council, Washington.*] Dutch Gld. 14.00 (paper). ii + 157 pp.; ill. 1955.

Not since L. A. Borradaile's little paper "On the Classification of the Decapod Crustaceans" appeared in 1907 has the taxonomy of any major group of decapod crustaceans been completely reviewed. L. B. Holthuis not only brings the Borradaile classification up to date for the caridean and stenopodidean shrimps, but his contribution also extends far beyond the scope of that earlier classic. In addition to the keys to the superfamilies, families, and genera, complete synonymies of all taxonomic categories are listed, the type species of each genus is designated, and a figure of a species of each genus is given. The publication is therefore both a guide to the non-penaeid shrimps for the general biologist and a significant milestone in carcinological literature.

The only improvement in the paper that comes to mind would have been the addition of page references in the key to the families and superfamilies. The families are arranged in systematic order in the body of the text, not in their order of appearance in the key; and it is difficult to follow from the family key to the generic keys, especially when one finds that the index is limited to generic names only. This is a minor oversight, however, and one that most users will enjoy correcting in their personal copies. Those familiar with the reputation of L. E. Holthuis as the leading decapod specialist of our time, and as an unsurpassed bibliographic detective, will not be surprised at the general flawlessness of this paper. Because of it, his fame will be more widely recognized.

FENNER A. CHACE, JR.

HIPPIDEA ET BRACHYURA OUEST-AFRICAINS. *Mém. Franç. Afr. Noire, No. 45.*

By Théodore Monod. Institut Français d'Afrique Noire, Ifan, Dakar. 3000 fr. (paper). 674 pp. + 1 folded map; ill. 1956.

In his introductory remarks, Théodore Monod expresses regret that circumstances have restricted this study to a regional one. No apologies are necessary. This is a monumental revision of the 4 species of hippa-like crustaceans, and 212 species and subspecies of brachyuran crabs, thus far known from the area between Mauritania and Angola. More than 6,000 specimens of 167 species in the collections of the Institut Français d'Afrique Noire and the University College of the Gold Coast provided unequaled material for the preparation of such a volume. Excellent drawings by Nicolas Hallé, as well as by the author and others, make up the 884 text figures which admirably supplement the keys and taxonomic discussion. The figures of the male sexual appendages of 100 of the crabs are most important contributions to our knowledge of brachyuran relationships.

Comparison between this volume and André Capart's report on the Brachyura of the Belgian West African expeditions of 1948–49 is inevitable. The latter paper, published in 1951, is concerned chiefly with the sublittoral species, whereas Monod's monograph is based, for the most part, on shore collections. All but 4 of the 100 species listed by Capart, however, are included in the present volume, 22 of them under different names.

There is little doubt that this publication will be the authoritative one on the marine crabs of West Africa for a long time to come, and most carcinologists

will agree that it fully answers Monod's introductory question: "A défaut de révisions générales, souvent en pratique impossibles, ne peut-on penser qu'il puisse y avoir place encore, comme je l'ai cru, pour des révisions régionales qui, à condition de se vouloir attentives et critiques, pourront rendre service?"

FENNER A. CHACE, JR.

A TEXTBOOK OF ENTOMOLOGY. *Second Edition.* *By Herbert H. Ross. John Wiley & Sons, New York.* $7.75. xi + 519 pp.; ill. 1956.

The following are the premises on which I would base an appraisal of a textbook for an introductory course in entomology. (1) The course should be preceded by a general course in biology or zoology. (2) Presenting the *principles* of entomology to students who do not know the *facts* is a sterile form of pedagogy. (3) Students taking the course will observe and collect in the field the insects which they will subsequently identify in the laboratory.

From the first premise it follows that no pages will be wasted on non-insect arthropods nor on the elements of paleontology, biogeography, or ecology. From premise (2) it follows that after the necessary introductory chapters on the anatomy, physiology, and metamorphosis of insects, the book will be devoted exclusively to accounts of the orders and common families, including their morphology, taxonomy, habits, and ecology. There won't be space for any "luxury" chapters, simply because the number of species of insects is greater than the number of species of all other organisms combined. From premise (3) it follows that the book will contain keys to nearly all North American families. The *common* families alone will not suffice, because any adequate student collection will include uncommon families.

How does the book under review compare with my ideal? One must admit, not very favorably. Only 40 per cent of the space is devoted to the orders and families. The other chapters (with approximate proportions are: Growth of North American Entomology (5%); Arthropoda: Insects and their Allies (5%); External Anatomy (8%); Internal Anatomy (4%); Physiology (11%); The Life Cycle (8%), half of which is strangely devoted to food habits and social insects; Geological History of Insects (4%); Ecological Considerations (8%); and Control Considerations (6%).

Then there are minor irritants. The style, at least in the first chapter, is somewhat peculiar. Six figures are poorly reproduced. There are some pointless splittings and lumpings of orders. Biogeography gets a token treatment of half a page, including a map of the world and a 5-line paragraph; it could just as well have been omitted. And so on down my list of two dozen items.

Yet in spite of all my strictures, I still regard this as a good book. The treatment of principles is generally excellent; the text is readable; the illustrations are generally good; and the keys—to *common* families—are workable and well illustrated. If one desires a condensed combination of families and principles, he can hardly do better. As for me, I shall seek something closer to my ideal.

GEORGE C. WHEELER

ANNOTATED CATALOGUE OF AFRICAN GRASSHOPPERS. *By H. B. Johnston; preface by B. P. Uvarov. Cambridge University Press, New York.* $18.50. xxii + 833 pp. 1957.

This is in no sense a taxonomic revision of the grasshoppers of Africa. It is a list of the species that have been recorded (over 2,000), with complete bibliographic references for each species which are conveniently classified according to whether they provide descriptions, figures, or data on morphology, ecology, bionomics, economic importance, and geographic distribution. All taxonomic synonymy published before 1953 is included, but there is no new synonymy. Location of the type specimens is given, where known. The bibliography includes 981 titles.

The laborious task of analyzing this mass of published information appears to have been carried out with care. B. P. Uvarov is to be credited with the systematic arrangement of the genera and higher categories. The families Eumastacidae, Pneumoridae (the latter a group confined to Africa), and Acrididae are included; but the grouse-locusts (Tetrigidae) are not. Data on the geographic distribution of the species is by country or political subdivision, not by zoogeographical regions.

This publication has been sponsored by the Anti-Locust Research Centre, because of the potential economic importance of non-migratory grasshoppers in areas of Africa which are being developed agriculturally. Since grasshoppers are being increasingly used for ecological, physiological, biochemical, and cytological studies, one may hope that the growing universities of Africa will make use of the rich grasshopper fauna available to them.

M. J. D. WHITE

AMERICAN MOTHS OF THE SUBFAMILY PHYCTINAE. *U. S. nat. Mus., Bull. 207.* *By Carl Heinrich. Smithsonian Institution, Washington.* $5.50. viii + 581 pp.; ill. 1956.

This monumental taxonomic volume represents 25 years of labor and the culmination of the career of the

author, who died soon after completing the manuscript. It is taken for granted that the reader will be aware that this group of moths belongs to the Pyralididae, or snout moths, of some 10,000 known species, many of which are of economic importance. Included in this study are 194 genera, 619 species, and 21 local races, all from the Americas. Of these, 60 genera, 81 species, and 8 races are described as new, yet represent only a fraction of the undescribed material available, chiefly from tropical America, but consisting mainly of females. That the distributional records are based almost entirely on specimens examined by the author enhances the accuracy of the book, especially since in a great many cases the genitalia of the holotypes were studied.

Keys to the groups, genera, and species are based upon the wing venation and the genitalia; they are arranged more for practical use than for phylogenetic understanding. Following a very brief introduction, the bulk of the work is composed of concise descriptions of genera and species. For the latter, mention is made of the type locality and food plant, if known.

A 13-page check-list of the American Phyctinae is followed by a section of 234 pages containing 1138 illustrations of venation and genitalia, the latter usually depicted in fine detail. An extensive index concludes the work.

The author attempts to bring together in linear arrangement those forms which show relationships in structure and development, but he notes that an incomplete knowledge of the subfamily results in a tentative disposition and that complete understanding must await the accumulation of much more information. Heinrich humbly concludes, "We don't know which forms evolved from which, or how. We weren't there. We may surmise; but the guess of one ignoramus is as good as another, and there is nothing to be gained from either. I have had to be content with a mere revision. Would that it were more worthy." But the author is hardly responsible for the lack of data he deplores, and the volume is recognized as an important contribution to the literature of the Lepidoptera.

RALPH W. MACY

INSECTS AND SPIDERS. *A Book of Keys with Biological Notes.*

By C. P. Friedlander and D. A. Priest. Philosophical Library, New York. $2.75. viii + 124 pp.; ill. 1956.

This little book—it will actually fit in a pocket—is designed for "middle and upper-school classes," for "the first year of a general biological degree course," and for "the layman who is prepared to take more trouble than is required to follow some of the more popular books on identification." About a hundred common families of insects and eighteen families of spiders are covered. The Lepidoptera are omitted. The workable keys are illustrated with simple but appropriate sketches and are followed by notes on the families. Only adult insects more than 3 mm. long are keyed; a hand lens (8X) is required.

This book should prove very useful for fieldwork in Britain, but much as I admire it I cannot recommend it without reserve for use in the United States and Canada. Some two dozen of our common and/or conspicuous families are lacking. Several of the superficial key-characters would prove completely baffling. For example, the cuckoo wasps (Chrysididae) are keyed as having a "brilliant metallic, red and golden lustre;" our species are metallic blue or green and would key to the Scoliidae. Some of the family names may cause confusion: the houseflies (Muscidae) are placed in the Anthomyiidae; the flesh flies (Sarcophagidae) and blow flies (Calliphoridae) are included in the Tachinidae.

GEORGE C. WHEELER

HANDBOOK OF AMPHIBIANS & REPTILES OF KANSAS. *Second Edition. Univ. Kansas Mus. nat. Hist. misc. Publ. No. 9.*

By Hobart M. Smith. University of Kansas Press, Lawrence. $4.00 (cloth); $1.50 (paper). 356 pp.; ill. 1956.

This is a well-prepared guide to the herpetofauna of Kansas. Its utility and value are attested by the fact that a second edition was required within a half-dozen years of its first appearance. The book presents a fairly standard treatment of its subject. After some useful introductory material, there is a species-by-species account of the amphibians and reptiles known to inhabit the state. This is followed by short statements, with photographs, of extra-limital species; a glossary; an extensive list of literature; and an index.

There are a number of identification keys, which appear to have been carefully organized. The accounts of individual species include a reference to the name as used, the geographic range, a description, recognition characters, habits, and habitats. The forms are treated on the specific level and, if more than one race occurs in the state, they are discussed in appendices to each species account. Most of the forms are illustrated, although not always with Kansas specimens, and in at least one case, a specimen of a race not occurring in the state has been used. In addition to a spot map of the distribution in Kansas, a generalized map of the total range of each species is supplied. The maps for the Wood Frog and the Narrow-Mouthed Frog are, unfortunately, exchanged. I have found but three other lapses, none of which is serious.

In utilizing previously published records of distribution, a synthesizer can be extremely restrictive. Such

a person would not include questionable records, from localities outside the natural geographic range, that might have their origins in introductions, misidentifications, or mislabeling. Smith has apparently not been as restrictive in this matter as might be preferred.

The University of Kansas Museum of Natural History has continued to make a useful book available. Smith is a highly skilled specialist in his field, and is to be commended for taking time from his studies to prepare this excellent, semi-popular handbook.

ARNOLD B. GROBMAN

BIRDS OF THE CHICAGO REGION. *Special Publ. Number Twelve.*

By Edward R. Ford. The Chicago Academy of Sciences, Chicago. $1.50. viii + 117 pp. + 2 pl. 1956. There have been several publications on the birds of the Chicago region, but the present one is the best. It is not only more up to date, but also more critical. Many individuals are responsible for the field data, the editing, and the supervision that goes with a cooperative work such as this. E. R. Ford, who undertook the preparation of this revised check-list, died before it was completed, but as a tribute to his memory, he alone is credited with the authorship. The Chicago region as here delimited extends from Racine County, Wisconsin, to Berrien County, Michigan, and goes as far south as Kankakee and Rensselaer, so that the value of this book is not limited to residents of the city of Chicago. In addition to the regular list of birds, there is a hypothetical list, a list of references, indices to common and scientific names, a map, a gazetteer, and a memorial tribute to Edward R. Ford. This comprises a competent and useful local list.

HENRI C. SEIBERT

PRIMATOLOGIE. *Handbuch der Primatenkunde. I. Systematik, Phylogenie, Ontogenie.*

Edited by H. Hofer, A. H. Schultz, and D. Starck. S. Karger, Basel and New York; [Albert J. Phiebig, White Plains]. $45.25. xxiv + 1063 pp.; ill. 1956. This book is the first of about five projected volumes on the biology of the order Primates, with particular emphasis on morphology, although a few subjects basically physiological in nature will be included (as, in this first volume, reproductive biology, developmental processes, and serology). It represents a unique and monumental undertaking for primatology, both in its comprehensive scope and in the participation of so many authors, each of whom is a recognized authority on the subject on which he writes. All other similar works in this field have been far less ambitious (excepting only, perhaps, the current series from the pen of Osman Hill), and have been of single authorship.

The chapters of this first volume follow: Taxonomic review of the order (Walter Fiedler); Paleontology and evolution, especially of the non-hominoid primates (A. Remane); Fossil history of the Hominoidea (Gerhard Heberer); Reproductive biology (J. W. Harms); Gestation and birth (J. W. Harms); Early development and placentation (Dietrich Starck): Postembryonic age changes (Adolph H. Schultz); Pathology, teratology, and twinning (Adolph H. Schultz); and Serology (P. Kramp). An extensive list of references to the literature is appended to each chapter.

Fiedler's extremely useful and generally sensible revision of primate taxonomy, although one may disagree with it on some points, is certainly to be welcomed, for such a revision has been long overdue. The inclusion of the tree-shrews in the order Primates, although apparently fashionable at the moment, is certainly open to question. Yet it must be admitted that one cannot properly deal with primates without considering these animals, however they may be classified.

The paleontological sections by Remane and Heberer are useful summaries of current knowedge and opinions in this field. Heberer's penchant for new and altered terminology that suits his own interpretations, without due regard for the taxonomic rule of priority—as when he substitutes the generic name "Australanthropus" for *Australopithecus*—is to be regretted. Otherwise, his chapter is a stimulating, if somewhat biased, account which leaves one with the realization of how little is actually known about the critical stages of hominoid evolution.

The chapters on reproduction and early development by Harms and Starck are encyclopedic in their treatment, bringing together a mass of the scattered literature on these subjects. Nothing of comparable scope has hitherto been written for either area.

Schultz's two chapters are of their usual high quality. They consist not only of compilations and interpretation of the data in the literature—a large proportion of which have been contributed by Schultz himself—but also of numerous new, hitherto unpublished observations. The concluding chapter, by Kramp, deals largely with precipitins and "proteale" fractions. The blood groups will be dealt with in a succeeding volume.

One is naturally tempted to compare this handbook with Hill's currently appearing series of volumes on the primates—but such a comparison, as John Donne might have said, would be "odious." Hill's excellent books are the product of a single individual, with all of the accompanying disadvantages, as well as advantages, of such provenience; moreover, they deal with the primates by taxonomic groups, rather than by anatomical systems. The present work, on the other

hand, is quite the reverse, since it has been produced by a group of authors, and the subject is treated system by system, rather than group by group. A truly comprehensive treatment of the latter sort would be beyond the capacities of any single person, even were he a modern Leonardo da Vinci.

This initial volume of *Primatologia* merely serves to whet the appetite for more of this truly novel and outstanding contribution to the study of primates. Its format is worthy of its text, but the price ($45.25) is little short of appalling, and certainly will restrict its availability and, consequently and most regrettably, its usefulness.

WILLIAM L. STRAUS, JR.

ECONOMIC ZOOLOGY

ANNUAL REVIEW OF ENTOMOLOGY. *Volume 1. Edited by Edward S. Steinhaus; associate editor, Ray F. Smith. Annual Reviews, Stanford.* $7.00. x + 466 pp.; ill. 1956.

This book might have been more appropriately entitled an "Annual Review of Applied Entomology," since 70 per cent of its pages are devoted to that branch. Not that I complain personally, for it affords me a relatively easy way of keeping up to date; but the economic entomologist might want more of the basic subject matter. It would have been even easier for me if the reviews had been modeled more on the plan of Imms' *Recent Advances in Entomology*. After all, what I need to know—as a "pure" entomologist—about air-blast spraying can be said in less than three pages—and just in case I should want more, a classified list of references would take care of my need. The agricultural entomologist already knows more about the apparatus than this review tells. If the editors find Imms too textbookish, they might at least provide a summary to each review. Then the reader could do more skipping in the next volume.

The titles for the 21 reviews are so apt that the table of contents will give the best summary in the fewest words: The Physiology and Biochemistry of Diapause (Lees); Insect Nutrition (Lipke and Fraenkel); The "Language" and Orientation of the Honey Bee (Frisch and Lindauer); The Stability of Scientific Names (Usinger); Some Aspects of Geographic Variation in Insects (Hubbell); Arthropod Resistance to Chemicals (Hoskins and Gordon); The Mode of Action of Insecticides (Kearns); The Chemistry of Insecticides (Martin); Persisting Insecticide Residues in Plant Materials (Gunther and Blinn); Repellents (Dethier); Soil Insects and Their Control (Lilly); Stored Product Entomology (Parkin); Apparatus for Application of Insecticides (Brann); Ecology of Forest Insects (Graham); Some Recent Advances in Apicultural Research (Butler); Insect Transmission of Plant Viruses (Smith and Brierley); Nonbiting Flies and Disease (Lindsay and Scudder); Veterinary and Medical Acarology (Fuller); Modern Quarantine Problems (Camp); The Fundamental Theory of Natural and Biological Control (Thompson); and the Effect of Pesticides on Balance of Arthopod Populations (Ripper). There are two indexes—author and subject—and more than two thousand literature citations.

The following passage in Hubbell's article may well prove to be the most quotable statement of 1956:

> There seems to me some danger that, in practicing the "new systematics," theory will often be prematurely accepted as fact and misapplied. Population systematics is now in fashion, and everyone feels obliged to speak its language and "explain" in its terms. There is a vogue for the latest in theory, as witness the rapid rise and decline of genetic drift as an explanation of all change in small isolated populations, and the faddish way in which new terms and new ideas are made into "catch phrases" to be dragged into every discussion. More serious, we begin to encounter in taxonomic papers the facile, patterned "explanation" based on analogy and bolstered by authority.

Minor flaws in the *Review* include some two dozen egregious "editorial" errors (spelling, punctuation, grammer, typography). The style of several reviews will give aid and comfort to the current critics of scientific writing; Huxleyan simplicity and clarity still need champions. My most serious criticism concerns the article by W. R. Thompson. It is a polemic, not a review, and therefore has no place in this volume.

Having unburdened myself of these few complaints, I conclude by saying that as a whole the volume is interesting, informative, and invaluable. For entomologists it is required reading; for other biologists it is to be highly recommended.

GEORGE C. WHEELER

CHEMISTRY AND USES OF PESTICIDES. *Second Edition. By E. R. de Ong. Reinhold Publishing Corporation, New York; [Chapman & Hall, London.]* $8.75. viii + 334 pp.; ill. 1956.

In 1948 de Ong published a book, *The Chemistry and Uses of Insecticides* (*Q.R.B.*, 25: 348. 1950). The new edition is brought up to date even to the extent of using the term "pesticide" instead of "insecticide." The book discusses the practical aspects of use and toxicology of the standard materials used today for insecticides, fungicides, weed killers, and wood preservatives. It should be useful to the practical man, the farmer, the county agent, and the teacher of agricultural workers.

J. G. HORSFALL

ANIMAL MORPHOLOGY

THE VERTEBRATE BODY. *A Shorter Version of the Second Edition.*

By Alfred Sherwood Romer. W. B. Saunders Company, Philadelphia and London. $5.50. viii + 486 pp.; ill. 1956.

The present volume was prepared in response to numerous requests for a volume shorter than the original, which was too lengthy for use in the limited time available in many courses. Its quality needs no recommendation beyond the eminence of its author. It is authoritative, clearly written, and well illustrated. In keeping with its purpose, no attempt has been made to create a reference text, the only bibliography being a 5-page appendix. This scholarly work should serve well as a textbook for a short, general zoology course.

F. N. Low

CONCISE ANATOMY. *Second Edition.*

By Linden F. Edwards. McGraw-Hill Book Company, New York. $7.50. xii + 502 pp.; ill. 1956.

In the present edition (first edition, *Q.R.B.* 25: 414. 1950) of this rather short textbook on anatomy, the general order of presentation has been retained, but some of the material on the nervous and circulatory systems has been rearranged. Principles of applied anatomy have been added at the end of many chapters. This book is a careful piece of work, not long enough or sufficiently detailed to serve as a primary textbook for medical students, and a bit too long and technical for non-medical students. It could well represent the anatomy text that is expected to be in the library of every biologist.

F. N. Low

ATLAS OF OUTLINE DRAWINGS FOR VERTEBRATE ANATOMY. *Second Edition.*

By Samual Eddy, Clarence P. Oliver, and John P. Turner. John Wiley & Sons, New York; Chapman & Hall, London. $3.25 (paper). 106 illustrations. 1955.

This book consists of a series of 109 titled but unlabeled drawings of selected parts of amphioxus (8), dogfish shark (27), sturgeon (1), gar (1), bowfin (2), necturus (21), and cat (49). They are neatly done and printed as line drawings on one side of heavy paper perforated to facilitate removal.

F. N. Low

THE DISSECTION OF THE CAT (*and Comparisons with Man*). *A Laboratory Manual on Felis domestica. Third Edition.*

By Bruce M. Harrison. The C. V. Mosby Company, St. Louis. $3.50 (paper). 217 pp.; ill. 1956.

The text of this work consists mainly of descriptions of the parts to be studied, some general statements about comparisons with man, and questions for the student to answer at the close of the various sections. The line drawings are labeled in the human drawings, but the labeling lines for the cat are left blank, to be filled in by the student. Numerous left-hand facing pages are left blank for notes. Designed for a course in vertebrate, comparative, or human anatomy in which cadavers are not available, this book should be adequate for its purpose.

F. N. Low

A WORKBOOK OF ANATOMY.

By C. P. Martin and S. M. Banfill. Scholar's Library, New York. $3.50 (paper). 142 pp. 1956.

This unusual volume comprises essentially a set of notes which "contain an outline of essential anatomical facts and in many places draw attention to the clinical importance of particular details." They are designed for the student's use in "lectures, laboratory and revision, and to save him the drudgery of taking endless hurried notes which are often lost, and nearly always are inaccurate and incomplete." The text is descriptive and the style telegraphic. There are no illustrations. Terminology is used freely to the point of inaccuracy. This does not appear to be a careful piece of work, and its usefulness, even for its stated purpose, is doubtful.

F. N. Low

HUMAN ANATOMY AND PHYSIOLOGY. *Fourth Edition.*

By Nellie D. Millard, Barry G. King, and Mary Jane Showers. W. B. Saunders Company, Philadelphia and London. $5.00. xii + 593 pp.; ill. 1956.

This is one of the numerous acceptable textbooks covering both anatomy and physiology at an elementary level and designed for use by nurses and other medical-technical groups. The new edition retains the over-all plan of the previous ones but includes additional introductory material and treats the nervous system early in the book, in the second section. This book should continue to enjoy popularity.

F. N. Low

HANDBOOK OF HISTOLOGY. (*Formerly "Handbook of Microscopic Characteristics of Tissues and Organs"*). *Fourth Edition.*

By Karl A. Stiles; introduction by Melvin H. Knisely. The Blakiston Division, McGraw-Hill Book Company, New York, Toronto, and London. $3.00 (paper). xiv + 240 pp.; ill. 1956.

This familiar aid to histological study is essentially in outline and tabular form with a few line drawings and blank pages for note-taking. In the present edition the text has been revised, and there are new parts on the interpretation of histological sections and on selected histological topics. The enlarged glossary has been made self-pronouncing, and the bibliography has been expanded. This useful supplement to histological textbooks should continue to enjoy popularity.

F. N. Low

LABORATORY DIRECTIONS FOR HISTOLOGICAL TECHNIQUE.

By Alfred Brauer. Burgess Publishing Company, Minneapolis. $1.75 (paper). iii + 46 pp. + 1 chart. 1955.

This simple, neat presentation of elementary histological technique is brief, but it is a commendably comprehensive presentation of its subject. It is printed on the right-hand pages only; the left-hand ones are left blank for notes. There are a few line drawings, and limited reference is made to the larger textbooks on technique. Although designed for a specific course, this manual should be flexible enough for general use in any undergraduate course in elementary histology. A quadruple folded page at the end, suitable for bulletin board posting, presents a résumé of the common methods of fixation, sectioning, staining, etc., and should be useful in any laboratory. This modest volume is a nice piece of work.

F. N. Low

BONE AND BONES. *Fundamentals of Bone Biology. Second Edition.*

By Joseph P. Weinmann and Harry Sicher. The C. V. Mosby Company, St. Louis. $13.75. 508 pp.; ill. 1955.

This is the second edition of a volume which first appeared in 1947. The review of the earlier text (*Q.R.B.*, 23: 257. 1948) can be referred to for general comments. The present edition has not been altered drastically, but some modifications and additions have been incorporated. The volume is devoted to the normal structure and growth and to the pathology of bone and bones, as studied from histological, x-ray, and clinical aspects. By far the most attention is devoted to pathological conditions affecting the skeleton.

No new chapters have been added, but new or expanded sections include discussions of histogenesis and the histology of the otic capsule, the grey-lethal mouse and the incisor-absent rat, multiple enchondromatosis, progressive diaphyseal dysplasia, generalized osteochondrodystrophy, osteopoikilosis, Sudeck's atrophy of bone, generalized hypertrophic osteoarthropathy, and chondrosarcoma.

The volume is well illustrated and well documented.

R. VAN REEN

RECENT ADVANCES IN THE STUDY OF THE STRUCTURE, COMPOSITION, AND GROWTH OF MINERALIZED TISSUES. *Ann. N. Y. Acad. Sci., Vol. 60, Art. 5.*

Edited by Roy Waldo Miner, consulting editor, Roy O. Greep; Roy O. Greep and Albert E. Sobel (conference co-chairmen), W. D. Armstrong, L. F. Bélanger, R. C. Greulich, S. B. Hendricks, H. C. Hodge, C. P. Leblond, P. L. Munson, W. F. Neuman, R. A. Robinson, D. B. Scott, J. H. Shaw, R. F. Sognnaes, M. V. Stack, O. R. Trautz, M. L. Watson, J. H. Weikel, Jr., and L. Wilkins. New York Academy of Sciences, New York. $4.00 (paper). Pp. 541–806; ill. 1955.

This is another, quite characteristic New York Academy report of a conference on a highly specialized subject. In a series of 14 papers, the mineralized tissues, bone and teeth, are discussed from the various approaches of accomplished investigators. An introduction opens the series, which is followed by a panel discussion. This report presents another good set of papers, many of them basically reviews of their authors' special fields. They are essential to all who are interested in mineralized tissues, but their usefulness outside of this specialty is necessarily very limited.

F. N. Low

THE MYOLOGY OF THE WHOOPING CRANE, *GRUS AMERICANA. Ill. Biol. Monogr., Vol. XXIV, No. 2.*

By Harvey I. Fisher and Donald C. Goodman. The University of Illinois Press, Urbana. $2.50 (paper). viii + 127 pp.; ill. 1955.

This monograph by two competent anatomists presents a very timely and thorough description of the myology of the Whooping Crane, one of America's vanishing bird species. Three specimens were available for dissection, and particular attention was devoted to individual variations. The text is divided into 8 sections

corresponding to anatomical regions, each being preceded by a very useful synonymy of muscle nomenclature. One hundred and twelve pages are devoted to descriptions of muscles and their innervation, and 6 pages to discussion of anatomical variations. The anatomical details are clearly depicted in 40 line-drawings. Of special interest are the semidiagrammatic illustrations of the brachial and sacral plexuses. Throughout the text, attempts have been made to clarify confusing problems relating to the homologies of avian musculature; pertinent literature has been cited in each case. Comparisons are made with other species of the genus *Grus* and the family Gruidae. No discussion of functional, phyletic, or taxonomic implications is included. This specialized study will be of interest primarily to students of avian morphology and taxonomy.

WADE FOX

A TEXTBOOK OF NEUROLOGY.

By H. Houston Merritt. Lea & Febiger, Philadelphia. $12.50. 746 pp.; ill. 1955.

This new textbook is written for medical students and physicians and is based on the author's conviction that neurology, previously most closely associated with psychiatry, is fast becoming allied to internal medicine. Recent advances in the latter field have projected their benefits to diseases of the nervous system previously interpreted as hereditary, and thus hopeless. There is a considerable indication that the influence of internal medicine will continue to extend itself into neurology. With this conception in mind, the author has constructed a careful and comprehensive account of clinical neurology. The text is clear and the illustrations, in many styles, good. Each section is followed by a very useful bibliography.

The judgment of this work must eventually be made, of course, by clinical neurologists. But the painstaking care with which it has been executed argues well for its eventual success.

F. N. LOW

ANIMAL PHYSIOLOGY

GENERAL ENDOCRINOLOGY. *Second Edition.*

By C. Donnell Turner. W. B. Saunders Company, Philadelphia and London. $8.00. xii + 553 pp.; ill. 1955.

The 2nd edition of this text differs from the first edition in many respects. Some parts have been rewritten, some rearranged, and some slightly enlarged; and the book as a whole has been brought up to date.

Specifically, a chapter on stress has been added. The chapters dealing with the pituitary gland and the adrenal cortex have been revamped; and sections dealing with biochemical aspects have been given greater play. Despite the latter addition, a student with limited biochemical background will require a supplementary biochemistry text in order to appreciate properly the interrelations of hormones with biochemical reaction mechanisms. The author has chosen to add to the second edition new photographs depicting cases of extreme endocrine disturbances. While this change may be welcomed by some readers, it represents a movement to conform with other textbooks of a similar nature, rather than a manifestation of the "rebellious spirit" to which the author (in the Introduction) attributes his disinclination to treat endocrinology as a clinical science. It is to be regretted that the space occupied by these pictures was not used to clarify by illustration other non-clinical topics. The text affords much opportunity for the latter.

Thus, while the volume is not distinguished by any great originality, the text is well-integrated, broad in its approach to the subject matter, and admirable in its emphasis on the comparative aspects of vertebrate and invertebrate endocrinology.

CLAUDE F. BAXTER

HYPOTHALAMUS AND THALAMUS. *Documentary Pictures.*

By W. R. Hess. Georg Thieme Verlag, Stuttgart; Intercontinental Medical Book Corporation, New York. DM 36.–; $8.60. x + 70 pp.; ill. 1956.

W. R. Hess began his studies of the physiology of the brain-stem in 1924. His first step was to develop a technique which would enable observations of suitable animals to be made without impairing the animals' freedom of movement by physical restraint or by anesthesia. The results obtained from studies of cats by this new technique were published in 1932, 1938, and 1949. These monographs, which summarize the research on the functions of the diencephalon, have already gained the status of classics in physiology. A number of illustrations showing examples of the responses elicited by the experiments discussed in the text were published in these monographs; but a wealth of material which could be presented as further evidence for the author's conclusions remained unpublished. Most of this material is now made available in the atlas. Findings are conveniently grouped here according to their functional significance. Since typical reactions of the cats are illustrated on the same page with sections of the brain-stem showing the lesions responsible for these reactions, the book can be used with great facility. For further information, the original cinematographic films, as well as serial sections of the brains, can be studied in Zurich.

The atlas is an indispensable tool for teachers and research workers in neurophysiology or neuropathology. In addition to such specialists, everyone interested in scientific documentation should study the book. The legends are in German and in English, and both illustrations and legends are models of clarity. The pleasing format of the atlas prompts one to congratulate the publisher for an outstanding job.

W. FLEISCHMANN

VITAMINS AND HORMONES. *Advances in Research and Applications. Volume 14.*

Edited by Robert S. Harris, G. F. Marrian, and Kenneth V. Thimann. Academic Press, New York. $10.00. xi + 486 pp.; ill. 1956.

The broad spectrum of vitamin and hormone metabolism, function, and interrelationships is becoming increasingly difficult to cover by reading current literature. This annual volume on vitamins and hormones helps keep one informed by presenting extensive reviews of several areas within the field. The current volume offers 8 chapters, two of which are devoted to vitamins and the remainder to hormones. Each chapter is written by an expert. In the present volume, the authors represent England, Scotland, Germany, and the United States.

The question of the synthesis of vitamins in the intestinal tract of nonruminant animals and the availability of these vitamins is discussed by O. Mickelsen. The influence of sulfonamides and antibiotics on animal growth is also covered in terms of intestinal synthesis.

Some aspects of vitamin A metabolism are treated by J. S. Lowe and R. A. Morton. Their discussion of the conversion of carotene to vitamin A considers the site of conversion, its mechanism, and the influence of other materials on it. The mode of action of vitamin A is also discussed, with some reference to current findings showing the presence of two unknown materials in the lipid unsaponifiable fraction from vitamin-A–deficient rats.

Two chapters are concerned with the hormonal control of carbohydrate metabolism. The regulation of carbohydrate metabolism in isolated tissues is reviewed by A. E. Renold, J. Ashmore, and A. B. Hastings. Experimental hyperglycemia not primarily due to a lack of insulin is presented by K. H. Shull and J. Meyer. A unique discussion by P. Carlson of biochemical studies of insect hormones covers the isolation, purification, and action of the hormones, and includes the work on the fascinating queen substances of bees and the social substance of termites.

Because of the ability of some steroids to form glucuronides, glucuronide metabolism is considered with reference to the steroid hormones, by G. A. Levvy. The hydrolytic enzyme β-glucuronidase, and the complex enzyme system accomplishing the synthesis of the conjugated glucuronides, are the main subjects of his review.

Two further aspects of hormone research are presented. J. A. Loraine discusses the bioassay of pituitary and placental gonadotropins in relation to clinical problems in man. S. H. Eppstein, P. D. Meister, H. C. Murray, and D. H. Peterson present the microbiological transformations of steroids and their application to the synthesis of hormones.

As in past years, this volume is well-documented and will be a valuable addition to the libraries of workers on vitamins and hormones.

R. VAN REEN

ANIMAL NUTRITION

SYMPOSIUM ON NUTRITIONAL ASPECTS OF BLOOD FORMATION, *1955. Proceedings of the Nutrition Symposium held at the University of Cincinnati, College of Medicine, Cincinnati, Ohio, October 22, 1954.*

Contributors: G. E. Cartwright, R. C. Crafts, G. W. James, III, T. H. Jukes, C. V. Moore, J. F. Mueller, R. F. Schilling, R. W. Vilter, J. J. Will and J. N. Williams. National Vitamin Foundation, New York. $2.50 (paper). i + 74 pp.; ill. 1955.

The papers in this volume were originally presented at the Nutrition Symposium held at the University of Cincinnati in 1954. They are reprinted from the *American Journal of Clinical Nutrition*, 3: 1–74 (1955).

Two papers deal with the role of minerals in blood formation. In discussing iron-deficiency anemia, C. V. Moore considers whether diet plays an important or a minor role in this type of anemia. The metabolism of copper, cobalt, zinc, and molybdenum in regard to hemopoiesis is briefly reviewed by G. E. Cartwright.

The importance and interrelationships of folic acid, vitamin B_{12}, and ascorbic acid are discussed in three papers. R. C. Crafts is author of a paper on the relationship of hormones to the utilization of essential nutrients in erythropoiesis. His brief paper is concerned with the ability of a combination of thyroxine, testosterone propionate, and a high protein diet to give a normal hemoglobin level and erythrocyte count in hypophysectomized rats.

Other subjects considered are: the use of antimetabolites and antibiotics as tools for research on blood formation; stercobilin and hematopoiesis; and management of hematopoietic disorders of human beings. Since each paper contains many current data and numerous references, the proceedings should be of value to nutritionists, biochemists, and physicians.

R. VAN REEN

A DICTIONARY OF DIETETICS.

By Rhoda Ellis. Philosophical Library, New York. $6.00. viii + 152 pp. 1956.

This compilation of terms related to nutrition and dietetics is unique in that it makes an attempt to define numerous materials, pathological conditions, vitamins, hormones, enzyme cofactors, etc., for both lay and professional people interested in nutrition. Simplified definitions are used throughout the volume, and no chemical formulas are presented. Many definitions are obscure or not strictly authentic, but this pitfall is difficult to avoid in trying to translate scientific data into popular terms.

Along with the brief definitions, the author provides several diets, including normal, salt-poor, and pregnancy requirements. He also lists food equivalents so that various fats may be substituted for one another. Similarly, equivalents for cereals, bread, vegetables, and meats are discussed. A table of the daily dietary allowances recommended by the Food and Nutrition Board of the National Research Council is included. The volume seems, however, too descriptive and too elementary for the specialist or student of nutrition.

R. VAN REEN

BIOPHYSICS AND GENERAL PHYSIOLOGY

PHYSICAL TECHNIQUES IN BIOLOGICAL RESEARCH. *Volume 1. Optical Techniques.*

Edited by Gerald Oster and Arthur W. Pollister. Academic Press, New York. $13.50. xiv + 564 pp.; ill. 1955.

This book constitutes a professional "reader's digest" of optical techniques; it is undoubtedly a godsend to biologists who wish to master principles and procedures without going to the basic literature in physics. The authors have selected the information which a biologist needs, and no more, and have presented it in elementary form. These volumes are offered as handbooks and guides to the manipulation, in the study of biological problems, of light and electrons by means of apparatus developed in the last two decades.

HUDSON R. ANSLEY

THERMODYNAMICS, *from the Classic and Generalized Standpoints.*

By Joseph Louis Finck. Bookman Associates, New York. $7.50. xvi + 224 pp.; ill. 1955.

This book is divided into two parts. The first 11 chapters constitute a review of "classic thermodynamics", with inculcative observations of what the author considers to be its defects. The last 11 chapters contain an extension of the author's "generalized thermodynamics," which he originally developed in a series of papers published from 1934–1949 in the *Proc. Amer. phys. Soc.* and the *J. Franklin Inst.*

In the Preface, the author states that the first 11 chapters are intended to be a text for advanced students and for those engaged in research in thermodynamics and allied fields. This first section "examines thermodynamics from the classic standpoint, bringing into prominence its difficulties and limitations." I found myself personally wearied by the difficulties and limitations inherent in the author's presentation of the classical viewpoint. His statements of the Second Law are the oldest possible, and embody none of the enhanced understanding of the past sixty years. There is a certain carelessness in his use of terminology. For example, the absurdity, dq is sometimes used for the heat absorbed by a system, as though it were a property of the system; and there are inconsistencies in the use of W and ΔW, Q and ΔQ in Chapters 7 and 8. Contrary to American practice, the symbols F and G are used for A and F, respectively, and cause some exasperation. Such defects, plus the absence of problems to work, make questionable the value of this book as an advanced text.

The author makes the point that "classic thermodynamics" limits itself to a consideration solely of reversible systems, which he terms "complete," whereas all real systems have some degree of "incompleteness" (irreversibility). Finck contends that in understanding a system it is essential to have a description of the degree of its "incompleteness," and he suggests that this description may be achieved by considering "the energy retained when it [the system] goes through an 'apparent' cycle process." This approach is applied to considerations of phenomena of friction, viscosity, electrical resistance, and other energy-dissipative properties of systems. The author claims, "A theory of catalysis develops from these considerations without injecting *ad hoc* assumptions." This section may be of value to those interested in comparing Finck's new theories with those of De Groot and Prigogine.

ENNIS C. LAYNE

BIOCHEMISTRY

ADVANCES IN ENZYMOLOGY *and Related Subjects of Biochemistry. Volume XVII.*

Edited by F. F. Nord. Interscience Publishers, New York and London. $11.00. viii + 556 pp.; ill. 1956.

The biologist needs no introduction to this series of personalized reviews of timely and interesting subjects by prominent workers in the fields.

In Volume 17, Alberty reviews Enzyme Kinetics in general and discusses the reaction mechanisms of some

half a dozen enzymes in particular. Chance and William discuss The Respiratory Chain and Oxidative Phosphorylation. Their treatment of this currently interesting field is based in part on observations made with the delicate and ingenious methods of Chance and his associates. Mandl and Neuberg review their findings in the field of Solubilization, Migration and Utilization of Insoluble Matter in Nutrition. Axelrod, discussing Enzymatic Phosphate Transfer, considers acetate, sulfate, carbon dioxide, and formate activation, among other things. Edelman reviews at some length The Formation of Oligosaccharides by Enzymatic Transglycosylation. Mahler writes on The Nature and Function of Metalloflavoproteins and discusses some twelve or fifteen enzymatic activities, including that of xanthine oxidase, which is discussed in much greater detail by De Renzo.

With great detail, Wanio and Cooperstein have written about Some Controversial Aspects of the Mammalian Cytochromes, but the controversial areas are not clearly indicated. De Bush, in discussing Metabolic Aspects of Chemical Genetics, a topic of growing interest to the biochemist, considers a number of specific gene-enzyme relationships and concludes that proof of a "one gene—one enzyme" hypothesis is impossible to attain at present. Jeener writes briefly on Ribonucleic Acid and Virus Multiplication. A cumulative index of Volumes I–XVII is included.

ENNIS C. LAYNE

ENZYMES: *Units of Biological Structure and Function. International Symposium, jointly sponsored by the Henry Ford Hospital and the Edsel B. Ford Institute for Medical Research, Detroit, Michigan, and held at the Hospital, November 1, 2, 3, 1955.*

Edited by Oliver H. Gaebler. Academic Press, New York. $12.00. xiv + 624 pp.; ill. 1956.

As in the case of similar affairs, many of our outstanding scholars and researchers in the field of enzymology attended this symposium and contributed toward making the occasion scientifically stimulating and constructive, a fact well reflected in this transcript of the meeting.

It is well recognized that the purpose of most biological symposia is best served by limiting attendance and publishing the proceedings, in order to extend to a wider audience the benefits derived from the meeting of keen minds. This course of action has been followed by an increasing number of institutions in recent years. It is not surprising, therefore, to find that many of the participants in the present symposium have, within a rather limited space of time, also contributed chapters to various Reviews, Annuals, Composia and Symposia, in which some of the data presented in Detroit have been reiterated or closely paralleled. Any comparative evaluation of this book must, therefore, be influenced primarily by the combination of subject matter which it contains and its relation to the interests of the individual reader.

Certainly, this is a book worth owning. It is edited with restraint and contains a wealth of information. It is divided into six parts, each composed of several chapters, extended comments, and general discussion. While the discussions were spontaneous, the comments appear to have been prepared in advance and often introduce additional topics.

Part I, on The Origin of Enzymes, deals with enzyme induction (J. Monod), cellular differentiation (B. Ephrussi), nucleic acid and enzyme synthesis (E. F. Gale), and the nature of enzyme-forming systems (S. Spiegelman). Part II explores the status of the gene-enzyme relationship, with major papers contributed by A. D. Hershey, R. D. Hotchkiss, N. H. Horowitz and Marguerite Fling, and C. Yanofsky. Part III, on Enzymes and Cell Structure, contains major contributions by G. E. Palade, A. L. Lehninger, E. L. Kuff, and G. H. Hogeboom, a chapter on nuclear products and nuclear reproduction (D. Mazia), and one on photosynthesis by chloroplasts (D. I. Arnon).

The connection between physiological function and enzymes is explored in Part IV and features topics involving actomyosin (W. F. H. M. Mommaerts), myosin and ATP (M. F. Morales), the excretory mechanisms (J. V. Taggart), visual excitation (G. Wald), and the emission of light (W. D. McElroy and A. Green).

Under the heading Cellular Energy Sources, Part V, electron transport systems are discussed, with specific reference to the cytochromes, succinic dehydrogenase, ADP interaction, and structural patterns. A separate chapter deals with hematin compounds in the metabolism of photosynthetic tissue. Major contributions to this section were made by E. H. Stotz, T. P. Singer et al., B. Chance, D. E. Green, and M. Kamen.

The final section, entitled Regulation of Enzyme Activity, considers such topics as permeability (B. D. Davis), drug action (J. H. Quastel), interference with nucleic acid metabolism (A. D. Welch), and the regulation of enzyme activity in muscle during work (C. F. Cori). The evening lectures, on The Future of Enzyme Research (L. Pauling), and on Mechano-chemical Coupling in Muscle (A. Szent-Györgyi), are also recorded. Author and subject indexes, both valuable for reference purposes, are included.

The list of other distinguished and active participants in this symposium who are not mentioned above, is impressive, and their sharp and timely comments help considerably in expanding, clarifying, and pinpointing the topics discussed by the main speakers. In short, for those who did not, but would have liked to, attend the symposium, this volume provides an authentic and stimulating experience.

CLAUDE F. BAXTER

MODERNE METHODEN DER PFLANZENANALYSE. *Four Volumes.*

Edited by K. Paech and M. V. Tracey. Springer-Verlag, Berlin, Göttingen, and Heidelberg. Vol. I: DM. 108. xviii + 542 pp.; ill. 1956. Vol. II: DM. 110. xiv + 626 pp.; ill. Vol. III: DM. 138. xiv + 761 pp.; ill. Vol. IV: DM. 145. xvi + 766 pp. ill. 1955.

Plant biochemistry has made remarkable advances during recent years largely because of the development of new and sensitive methods of separating, isolating, and identifying plant constituents. These methods are to be found in a number of languages and in a wide variety of journals. It was the purpose of the editors of this four-volume handbook of plant analysis to bring together all of these techniques and methods for analyzing plant tissue. They have succeeded remarkably well, and the 67 chapters (21 in German) are handled in a monographic style by experts in the field. Each chapter contains a complete bibliography, and each volume has an English-German, German-English subject index.

The work is of such magnitude that it is impossible to review critically each volume. Only the chapter headings of each volume can be listed. Volume I: Allgemeine Massnahmen und Bestimmungen bei der Aufarbeitung von Pflanzenmaterial; General Methods for Separation: Making and Handling Extracts; General Methods for Separation: Electrical Transport Methods; Multiplikative Verteilung; Chromatographische; Analyse in Säulen; Papier-Chromatographie; Colorimetric, Absorptimetric, and Fluorometric Methods; Refraktometrie und Interferometrie, Polarimetrie, Nephelometrie; Principles of Biological Assay; Methods Involving Labelled Atoms; Estimation of *p*H Values; Oxidation-Reduction Potentials; Gasometric Analyses in Plant Investigation; Cytochemical Methods; Mineral Components and Ash Analysis. Volume II: Mono- and Oligo-saccharides and Acidic Monosaccharide Derivatives; Acyclic Sugar Alcohols; Inosite und verwandte Naturstoffe; Ascorbinsäure; Phosphorylated Sugars; Starch, Glycogen, Fructosans, and Similar Polysaccharides; Cellulose and Hemicelluloses; Pektine; Chitin; The Analysis of Plant Gums and Mucilages; Glycosides as a General Group; Fats and Other Lipids; Volatile Alcohols, Aldehydes, Ketones, and Esters; Volatile Acids; Nichtflüchtige Mono-, Di- und Tricarbonsäuren; Non Volatile Mono-, Di-, und Tricarboxylic Acids; Lactones. Volume III: Die niederen Terpene (ätherische Öle und Harze allgemein); Pyrethrins and Allied Compounds; Triterpene und Triterpen-Saponine; Phytosterine, Steroidsaponine, und Herzglykoside; Carotenoids; The Determination of Rubber and Gutta in Plants; Simple Benzene Derivatives; Natural Tropolones; Ein- und Zweikernige Chinone; Natural Phenylpropane Derivatives; Lignans; Anthocyanins, Chalcones, Flavones, and Related Water-Soluble Plant Pigments; Lignin; Natürliche Gerbstoffe; Anthraglykoside und Dianthrone; Growth Substances in Higher Plants; Antibiotics. Volume IV: Peptides (Bound Amino Acids) and Free Amino Acids; Proteins; Seed Proteins; Methods of Determining the Nutritive Value of Proteins; Urea and Ureides; Chlorophylls: Analysis in Plant Materials; Haematin Compounds; Nucleic Acids, their Components and Related Compounds; Adenosine Diphosphate, Adenosine Triphosphate; Codehydrasen I und II; Thiamine and its Derivatives; The Alkaloids; Amine und Betaine; Pantothensäure and Coenzym A; Riboflavin, Folic Acid, and Biotin; Melanins; Blausäure-Verbindungen; Senföle, Lauchöle und andere schwefelhaltige Pflanzenstoffe.

The contributors have not presented tables showing where the various plant constituents are found in the plant kingdom, nor have they discussed the metabolism and possible biosynthetic mechanisms responsible for the formation of the various constituents. The handbook is concerned only with methods, and it is the most complete and up-to-date work available today. It is recommended without qualification to all workers who have occasion to analyze plant tissues.

G. R. NOGGLE

THE ALKALOIDS, *Chemistry and Physiology. Volume V: Pharmacology.*

Edited by R. H. F. Manske. Academic Press, New York. $9.50. x + 388 pp.; ill. 1955.

This volume is the last in a series dealing with the chemistry and pharmacology of the alkaloids. Nine chapters present the following discussions of pharmacologically related alkaloids: Narcotics and Analgesics (Hugo Krueger); Cardioactive Alkaloids (E. L. McCawley); Respiratory Stimulants (Marcel J. Dallemagne); Antimalarials (L. H. Schmidt); Uterine Stimulants (A. K. Reynolds); Alkaloids as Local Anesthetics (Thomas P. Carney); Pressor Alkaloids (K. K. Chen); Mydriatic Alkaloids (H. R. Ing); and Curare-like Effects (L. E. Craig). Also included is a chapter on the Lycopodium Alkaloids and one dealing with a miscellaneous group of unknown structure, both written by the editor. An examination of these chapters confirms what is indicated by the list of authors—that this volume represents the efforts of experts in these fields. I have found it to be a specialized textbook of value both as a reference work and a teaching aid.

C. JELLEFF CARR

NUCLEAR AND RADIOCHEMISTRY. *Revised Version of "Introduction to Radiochemistry."*

By Gerhart Friedlander and Joseph W. Kennedy. John Wiley & Sons, New York; Chapman & Hall, London. $7.50. x + 468 pp.; ill. 1955.

Those who considered *Introduction to Radiochemistry* (1949) a good textbook, will find that this second edition, which is renamed *Nuclear and Radiochemistry*, is even better. As a textbook it has the major assets of clarity and conciseness. Discounting one or two minor exceptions, the subject matter presented will require no elaborate amplification in the classroom, yet the questions appended to the end of each chapter offer both an opportunity to test comprehension and a starting point for discussion. Reference material is also provided. The earlier edition (*Q.R.B.*, 25: 106. 1950) has been vastly extended and brought up to date within the framework of the original chapters. In addition, the topics of nuclear reactors and cosmic rays are handled in two new chapters.

This book is aimed at the senior or graduate student in chemistry who has a sound foundation in physics, calculus, and inorganic chemistry. Yet its scope is such that it can also be heartily recommended to advanced students and researchers in the biological sciences who wish to acquire a background knowledge of the principles underlying instrumentation, mathematical evaluation, and production for radioisotopes and radiations.

CLAUDE F. BAXTER

MEDICINAL CHEMISTRY. *Volume II. A series of Reviews Prepared under the Auspices of the Division of Medicinal Chemistry of the American Chemical Society. Edited by F. F. Blicke and C. M. Suter. John Wiley & Sons, New York; Chapman & Hall, London.* $10.00. viii + 311 pp.; ill. 1956.

This volume—the second in the series—presents a discussion of the following subjects: Some Chemical Aspects of the Cardiac Glycosides (Arthur Stoll), with a supplement on the Isolation and Identification of New Glycosides (T. L. Johnson); Synthetic Estrogens (John A. Hogg and Jerome Korman); Analgesics, Arylpiperidine Derivatives (C. M. Suter); and β-Haloethylamine Adrenergic Blocking Agents, Chemistry and Structure-Activity Relationships (Glenn E. Ullyot and James F. Kerwin). There is a separate index for this volume. The major part of the volume (183 pages) is devoted to the synthetic estrogens. A table of classification of synthetic estrogens is provided with a bibliography that includes patents. The literature is covered to September, 1953. As in the first volume of this series, a successful attempt has been made to provide an encyclopedic coverage of the subject matter.

C. JELLEFF CARR

MEDICINAL CHEMISTRY. *Volume III. A Series of Reviews Prepared under the Auspices of the Division of Medicinal Chemistry of the American Chemical Society. Edited by F. F. Blicke and R. H. Cox; associate editor, L. A. Woods; assistant editor, Harriet Geer; 6 authors. John Wiley & Sons, New York; Chapmen & Hall, London.* $10.50. viii + 346 pp.; ill. 1956.

Volume III in this series is devoted to Methadone and Related Analgesics (Thomas P. Carney); Quaternary Ammonium Germicides (Peter L. de Benneville); Non-Mercurial Diuretics (Viktor Papesch and Elmer F. Schroeder); and Synthetic Analogs of Physostigmine (Arthur Stempel and John A. Aeschlimann). An index for the volume is provided. As in the other volumes in this series, each topic is presented in encyclopedic form with an extensive bibliography and patent references. The literature through August, 1953, has been covered by most of the authors.

C. JELLEFF CARR

MICROBIOLOGY

MICROBIOLOGY. *Second Edition. By Florene C. Kelly and K. Eileen Hite; foreword by G. M. Dack. Appleton-Century-Crofts, New York.* $7.50. xiv + 615 pp.; ill. 1955.

Although the authors claim to have incorporated the new knowledge in microbiology in the second edition of their textbook, in my own opinion, they have not succeeded in doing so. In undertaking the tremendous task of covering the whole field of microbiology, the authors fall short of achieving their goal. Although many advances in microbial physiology have made an impact on various disciplines of the field in recent years, the authors devote only 20 pages to this subject; yet, they spend 100 pages on a lengthy introduction to the microscopic world. Such omissions as those of the phenomenon of transduction, the role of iron in diphtheria toxin production and its consequences in the metabolism of the organism, the ability to transmit toxigenicity to a non-toxigenic organism, the immobilization test as an indispensable tool in eliminating biologic false positive reactions in the sero-diagnosis of syphilis, and many others too numerous to mention, are self-evident. It appears that emphasis has not been placed on fundamental concepts which should supply the basic foundation for the orientation of students in the field of general, as well as pathogenic, microbiology. Although the authors believe "in a conservative attitude, and that controversial material may best be presented at the discretion of the instructor," is it not a stimulus to the beginning student to get an eclectic viewpoint, even though such a viewpoint is sometimes controversial?

The textbook, however, is well indexed; has excellent photographs and diagrams; and, because of its wide coverage of the subject, should prove of worth in teaching a begining college or nursing course in microbiology.

MORTON M. WEBER

MICROBES AND US.

By Hugh Nicol. Penguin Books, Baltimore. 65 cents (paper). 272 pp.; ill. 1955.

This small and inexpensive book contains a large amount of interesting and valuable information, mainly on agriculture and soil conservation, with somewhat more of a chemical than a microbiological emphasis. Accordingly, the title is a bit misleading. A rather gloomy (but probably correct) picture is painted of the eventual effects of the exhaustion of the soil and of mineral resources, under the pressure of a heavily increasing world population. One is reminded of the phrase (attributed to H. G. Wells) about the world's being in "a race between education and disaster." The book can be highly recommended to the general reader (preferably one with some background in chemistry). Since the price is so low, it should be of very great value as background reading for college courses.

Aside from the main thesis of the book, all sorts of odd bits of information are included. For example, bacteriologists may be interested to learn that Serafino Serrati (after whom the genus *Serratia* was named) did *not* "invent a steam-boat at Florence before 1787," but built a model boat propelled by hot gases from its smokestack, and thus was a pioneer in jet rather than in steam propulsion. This comment corrects a misstatement in the author's earlier *Microbes by the Million*.

One mild "howler" was noted. In discussing bison on the western plains, it is stated (p. 112) that the "eastern part of North America produced no wild animal larger than a turkey." This does some injustice to the moose and bear of Canada and northern New England, as well as the deer which are common enough within 100 miles of New York City to be involved in occasional automobile accidents! Nevertheless, such errors are few, and as a thoughtful plea for better agriculture, the book is of high merit.

WALTER C. TOBIE

MICROBIOLOGY, *General and Applied. Second Edition. By William Bowen Sarles, William Carroll Frazier, Joe Bransford Wilson, and Stanley Glenn Knight. Harper & Brothers, New York.* $5.75. xiv + 491 pp.; ill. 1956.

The new edition of this book (*Q.R.B.*, 27: 232. 1952) can be classified as perhaps an "intermediate" approach to microbiology, since it is neither elementary nor advanced. As the title implies, it covers the whole field of microbiology, with consideration of both the medical and the non-medical aspects, and is presumably used by the authors as a textbook in their courses at the University of Wisconsin. It seems a good, solid, conventional work, written, unfortunately, in a somewhat pedestrian style. No glaring errors or misinterpretations were observed, but on the other hand, no particular signs of animation appear anywhere in it. We shall have to classify it as "just another text on microbiology."

WALTER C. TOBIE

MICROBIOLOGY *with Applications to Nursing. Second Edition. McGraw-Hill Series in Nursing.*

By Catherine Jones Wilton. The Blakiston Division, McGraw-Hill Book Company, New York, Toronto, and London. $6.00. xiv + 620 pp.; ill. 1956.

According to the Preface, "this book is designed as a text for students in schools of nursing and other medical arts," apparently in and around Boston, to a large extent. The Boston tradition of scholarship is well upheld, since the subject matter is much more comprehensive, solid, and advanced than that in most books intended for the training of nurses in bacteriology and related fields. In addition, each chapter is followed by a list of titles for suggested reading, sometimes books and sometimes articles in journals, a most constructive idea if the students have the time and opportunity for such a follow-up. The index seems excellent. Those interested in instructing nurses and others in medical microbiology would do well to examine this book themselves.

An incidental (and perhaps trivial) comment is that there seems to be no general agreement on van Leeuwenhoek's first name. It is given in different textbooks as "Anton," "Antonie," "Anthony," and no doubt other variations can be found. The present work gives it as "Antonj." This minor point deserves to be clarified and perhaps noted in some learned journal, such as *Isis*.

Another minor comment (applicable more to the S.A.B. charts than to texts on bacteriology) might be made in regard to the difficulty encountered in classifying growth and colony characteristics of bacteria. It is difficult indeed to attempt to differentiate (for example) between "saccate" and "napiform" liquefaction of gelatin, or between "raised" and "convex" colonies (pp. 70–71). Simplification in this field appears desirable. Until accomplished, textbooks and students will have to grapple with the present confused system.

WALTER C. TOBIE

THE TUBERCLE BACILLUS, *in the Pulmonary Lesion of Man. Histobacteriology and its Bearing on the Therapy of Pulmonary Tuberculosis.*

By George Canetti; foreword by Rene J. Dubos and Walsh McDermott. Springer Publishing Company, New York. $8.50. xii + 226 pp.; ill. 1955.

This is an enlarged and revised translation of the original French edition of 1946 (*Q.R.B.*, 25: 353. 1950). It is of particular value in coordinating knowledge of the histological and pathological changes with knowledge of the infecting organism. In other words, the behavior of *Mycobacterium tuberculosis* is considered both in vivo and in vitro. In this respect, it should be of great value both to the clinical physician and to biologists and chemists, who necessarily study the organism either in laboratory animals or in test tubes.

When the original French edition of 1946 appeared, the chemotherapy of tuberculosis was only in its beginning stage. The present edition brings this aspect well up to date, with a careful consideration of the mechanisms of action of streptomycin, *p*-aminosalicylic acid, and isoniazid. These drugs appear to be mainly of value as supplements to rest and surgical treatment.

The translation is skillful and smooth. There is an excellent bibliography, and an adequate index. Accordingly, the book can be recommended as an outstanding work in its field.

WALTER C. TOBIE

IDENTIFICATION OF ENTEROBACTERIACEAE.

By P. R. Edwards and W. H. Ewing. Burgess Publishing Company, Minneapolis. $4.00 (paper). xii + 179 pp.; ill. 1955.

This work, excellently reproduced by offset and spirally-bound, is not (like most of its kind) an elementary classroom laboratory manual, but is instead more a reference manual in a specialized field. If reproduced by conventional printing processes, the price would undoubtedly be much higher, and both the authors and the publishers can be congratulated on having produced such a fine piece of work at a very reasonable cost.

As stated in the Preface, the Enterobacteriaceae consist of a large number of interrelated types in which the nice conventional separation into sharply distinct species cannot be made with any degree of satisfaction. Instead, it is necessary to designate each isolate by its biochemical and serological characteristics as a "type" rather than as a "species." This is a far cry from long ago, when (along with other undergraduate students) I strove in vain to fit cultures into the Procrustes' bed of species classifications laid down by the second edition of Bergey's *Manual* of 1925! There were always a number of strains from any sample of milk, water, or sewage that just would not fit in anywhere, even on the basis of very simple fermentation reactions. All this has now been changed, or is being changed, and what has been lost in simplicity has been gained in accuracy. This manual should help greatly in clarifying what is at best a difficult situation.

WALTER C. TOBIE

MECHANISMS OF MICROBIAL PATHOGENICITY. *Fifth Symposium of the Society for General Microbiology, held at the Royal Institution, London, April, 1955. Cambridge University Press, New York.* $5.00. x + 333 pp.; ill. 1955.

The British Society for General Microbiology, through its annual international symposium, has once again produced an excellent contribution to a most interesting and provoking problem in microbiology. This volume, the fifth in the series, is devoted to mechanisms of microbial pathogenicity. It includes the following articles: The Meaning of Pathogenicity, by A. A. Miles; The Role of Toxins in Pathology, by W. E. van Heyningen; The Pathogenesis of Diphtheria, by A. M. Pappenheimer; On the Biochemical Mechanism of Action of Gas-gangrene Toxins, by M. G. Macfarlane; Botulinum and Tetanus Toxins, by G. P. Wright; Properties and Structures of Tubercle Bacilli concerned in their Pathogenicity, by R. J. Dubos; Studies on the Chemical Basis of the Pathogenicity of *Bacillus anthracis* using Organisms Grown *in Vivo*, by H. Smith and J. Keppie; The Basis of Virulence for Mice of *Pasteurella pestis*, by T. W. Burrows; The Pathogenicity of Protozoal and other Parasites, by F. Hawking; The Comparative Pathogenicity of Protozoa in their Vertebrate and Invertebrate Hosts, by P. C. C. Garnham; The Pathogenicity of Plasmodia and Entamoeba, by B. G. Maegraith; Host-parasite relations and Pathogenesis in Infections with *Entamoeba histolytica*, by C. A. Hoare and R. A. Neal; Pathogenicity of Fungi in Man and Animals, by G. C. Ainsworth; Pectic Enzymes Secreted by Pathogens and their Role in Plant Infection, by R. K. S. Wood; The Role of Toxins in the Etiology of Plant Diseases caused by Fungi and Bacteria, by P. W. Brian; and Studies on the Mechanism of Invasion of Plants by Vascular Pathogens, by W. G. Keyworth.

It is gratifying to find that a discussion of this nature has reproduced, in a volume of no more than a few hundred pages, the essence of what is known about the host-parasite relationship in disease without relying upon inconclusive discussions. Although some speculation, a necessity in such a symposium, is employed, most of the conclusions are based on good experimental data. In addition to being an excellent summary of what is actually known about the subject, the symposium poses many provocative questions which should stimulate both the student and the investigator to

explore these little understood areas. This book is highly recommended to all microbiologists, biochemists, and biologists in general who are concerned with host-parasite relationships.

MORTON M. WEBER

HEALTH AND DISEASE

MEDICINE IN A CHANGING SOCIETY. *Lectures to the Laity, No. XVIII. The New York Academy of Medicine.*

Edited by Iago Galdston. International Universities Press, New York. $3.00. x + 166 pp. 1956.

The New York Academy of Medicine presents, in this volume, the eighteenth series of Lectures to the Laity. Under the general title, *Medicine in a Changing Society*, the 5 included papers present a fairly broad panorama of research in mental health as it is related to problems of emotional adjustment in an ever-changing order of society.

In the lecture Adventure and Security in a Changing World, Franz Alexander sets the stage for the subsequent discussions by pointing to the trend in progressive societies away from adventure and toward security. This trend, if allowed to run its natural course, will eventually stifle experimentation and creativity and pose a threat to further advancement in civilization. Reminding us of some ancient civilizations which fell as a result of such a trend, Alexander sounds a warning against the social sterility that is apt to creep into a society overridden by a growing sense of insecurity.

John A. Rose next discusses Changes in Family Life and Mental Health, noting the strong tendency of pediatricians and the school systems to take over the complete rearing of modern children. A vigorous plea is made for a return to home and parental influence in the physical, mental, and social development of our children.

The third paper, by William Malamud, deals with Organic Factors and Personality Functions. Taking a good look into each end of the so-called "psychosomatic telescope," Malamud indicates not only the traumatizing effect of organic disease upon the personality, but also the influence of psychological factors upon the anatomy of disease as well as its importance in the prevention or minimization of the effects of disease.

W. Horsley Gantt presents the laboratory work that has led to an understanding of Nervous Breakdown, and demonstrates the importance of interpreting the "observer-subject" or "physician-patient" relationship in any experimental or clinical setting.

The series is concluded with Iago Galdston's Salerno and the Atom, a brilliant discourse on the need for a modern philosophy of health to encompass not only the absence of disease or the curing of a multitude of ailments, but also something of the ancient physician's understanding of man's harmonious relation to nature. Galdston proposes such a philosophy under the title, "Comprehensive Medicine," a concept that regards living as a sustained adventure and medicine as an ancillary of that adventure.

These papers provide a fascinating insight, from the medical point of view, into some of our society's most basic problems; as such, they can be profitably read by anyone. A list of references is appended to each paper for the benefit of those desiring to read further in these subjects.

B. AUBREY SCHNEIDER

SOCIETY AND MEDICINE. *Lectures to the Laity, No. XVII. The New York Academy of Medicine.*

Edited by Iago Galdston. International Universities Press, New York. $3.00. xii + 131 pp. 1955.

In its program of medical education for the public, the New York Academy of Medicine provides each year a series of Lectures to the Laity. The present series, following the pattern established in 1935 of presenting current advances in medical thought and practice, is concerned not so much with factual material as with orientation and guidance in the discernment and use of information provided to the public through the press, radio, and other public education media.

Although the six papers comprising this volume differ widely in subject matter, field of interest, and method of approach, they have been developed around a common theme: the concept of health and disease in its natural setting, i.e., in the human population. A further line of continuity runs through the series in that each lecture develops some facet of the general problem of heredity and environment as related to the prenatal or postnatal development of the child.

The timeliness and value of these discussions can be appreciated only when one considers the importance of sound physical, social, and psychological development of our citizens-to-be in determining the future welfare of our nation—and indeed, of the world.

B. AUBREY SCHNEIDER

GOOD HEALTH, *For You, Your Family, and Your Community.*

By Nelson S. Walke, Nathan Doscher, and Glenna Garratt Caddy. McGraw-Hill Book Company, New York, Toronto, and London. $4.75. xii + 415 pp.; ill. 1955.

This excellent college textbook on health is the sixteenth of the McGraw-Hill Series in Health Education, Physical Education, and Recreation. Written by two college health and physical education teachers and a

college physician, the volume is well adapted to the university classroom.

Stressing the positive aspects of health and well-being, the work is essentially a synthesis of the many disciplines (genetics, medicine, law, biometry, demography, epidemiology, disaster relief, dentistry, public health, anatomy, physiology, recreation, hygiene, exercise, nutrition, relaxation, rest, special senses, family life, adolescence, psychology, narcotics, and ethics) which have a bearing on health in a personal, family, or community setting. Recognizing that the essence of successful living is the sum total of daily experiences, the authors discuss a wide variety of topics, ranging from family planning and family budgets to the hazards of an atom bomb attack and the problems of the aged (geriatrics).

The text is well documented and well illustrated throughout. Each chapter concludes with a list of problems and a bibliography for further reading. A complete index is appended.

B. Aubrey Schneider

Better Health for Your Children. *A Medical Guide for Parents.*

By I. Newton Kugelmass. McGraw-Hill Book Company, New York, Toronto, and London. $4.50. x + 341 pp. 1955.

Home medical guides can be very useful if their users are aware that such books are designed to supplement, and not to substitute for, a physician's services. The author of the present volume makes this point perfectly clear, not only in the opening chapter, where he indicates the need for competent medical aid and consultation in emergency situations, but throughout the book by continuous references to home care before, during, and following the *physician's visit.*

Although the volume is entitled *Better Health for Your Children*, there is very little positive teaching to be read, absorbed, and applied over the "long haul" in the maintenance of good health. The book is designed instead for easy reference in assessing a multitude of ailments as they arise in the daily lives of growing children.

Beginning with some of the general principles of first aid and home nursing care, Dr. Kugelmass develops a well-organized compendium of the signs and symptoms of a long list of childhood ailments, and indicates the prognosis which can be expected if the parent will follow sound medical advice and instruction. Full consideration is given to the important part the parent must play in bringing the child through a serious illness or injury, back to a full and vigorous state of health and well being.

Based on a wide background of pediatric practice, the work is completely authoritative, though written in non-technical language. A detailed index enhances the value of the book as a reference volume.

B. Aubrey Schneider

Your Health Today.

By W. W. Bauer. Harper & Brothers, New York. $5.00. xvii + 514 pp.; ill. 1955.

In preparing this excellent textbook, the author had two paramount objectives in mind: (1) development of a meaningful definition of health and (2) presentation in a manner that would stimulate concepts and attitudes rather than simply impart a body of factual knowledge. The work shows a high degree of success in the achievement of both aims.

Starting with the premise that health is a way of life and not an end in itself, the author tentatively accepts the definition of health promulgated by the Joint Committee on Health Problems in Education of the National Education Association and the American Medical Association, which, stripped of its formal phrasing, reads about as follows: "Health is that condition of the human organism that permits one to live happily and successfully. It favors efficiency, but does not assure it. It helps toward attaining the goals and ambitions of life. The Committee thinks that even a handicapped person can be healthy, in this sense." From this, Bauer distills his own informal definition, that "health is feeling well in body, mind and spirit, with a sense of reserve power"—an attitude that is probably expressed even better in the following sentence from his Preface to the volume: "The indomitable spirit with a broken spine is a better man than the Adonis with a wishbone where his backbone ought to be." This philosophy will come as no surprise to the countless so-called "handicapped" persons in our midst who have always known that, in order to enjoy life, they must think of themselves as essentially healthy persons, regardless of what their physicians tell them or of what their neighbors think!

Bauer's method of presentation is a departure from the time-honored pattern of identifying man as an anatomical structure and a physiological mechanism, subject to disease, accident, and death. This author attempts to help his reader meet, in a reasonably happy frame of mind, the challenges of physical, mental, and emotional health. Each chapter of the book opens with a series of questions entitled "Do You Believe?"; proceeds through a lively discussion designed to encourage the student to arrive at his own conclusions; and ends with a brief list, "The Ignorance Curtain," of common mistaken beliefs, some of which the author hopes have been improved or corrected as a result of having read the chapter. The writer thus encourages the development of a philosophy of life which precludes blind submission to a set of rules for health, but instead one

which is based upon a sound, common-sense, individualized approach to the requirements of satisfactory living and a healthy disregard for the din of daily bombardments by fadists, quacks, and charlatans in the name of "good health."

B. AUBREY SCHNEIDER

MEN WITH GOLDEN HANDS. *A Book of Surgical Miracles.*

By E. H. G. Lutz. Appleton-Century-Crofts, New York. $3.75. ix + 269 pp. 1956.

In this book, each of 15 surgical cases is carried to a successful conclusion. Each is dramatically, at times, heroically, narrated by various members of the operating team. Sometimes the surgeon himself tells the story; other incidents are described by the intern, anesthetist, nurse, or radiologist. This book will appeal to anyone interested in medicine, particularly in the field of surgery. A layman, perhaps, will find the "unusual cases" much more engrossing than will a practicing surgeon.

ROBERT G. CHAMBERS

POLIOMYELITIS.

Contributors: Robert Debré, Darline Duncan, John F. Enders, Matthieu-Jean Freyche, Sven Gard, James Gear, W. McD. Hammon, Hilary Koprowski, H. C. A. Lassen, Johannes Nielsen, John R. Paul, A. M.-M. Payne, A. J. Rhodes, W. Ritchie Russell, A. B. Sabin, Stéphane Thieffry, and W. Wood. World Health Organization, Geneva. $8.00 (paper). 408 pp. 1955.

This volume is the latest in the monograph series made available by the World Health Organization. It includes contributions by 17 outstanding investigators.

The major topics covered are epidemiology, clinical aspects, virology, immunology, and control of poliomyelitis. Under the first of these is an excellent review of current knowledge of polio epidemiology in both urban and under-developed areas, with an analysis of the trends during recent years. The review of clinical aspects includes detailed information, based on data collected during the epidemic of 1952 in Denmark, concerning management of the respirator patient. The section on virology includes descriptions of many of the techniques of virus cultivation in tissue culture and of the application of virus cultures in further study and possible control of poliovirus infection.

Although there have been important advances in each of the above areas since the preparation of this volume, the advances in immunology and control have been the most extensive and have made these two sections of the book seriously out of date. The data regarding immunization with formalinized vaccine are limited to early trials, since experience in the use of this vaccine in widespread field tests and during epidemics was gained after the preparation of these manuscripts. Considerable further data have also become available regarding the potential value and risks of using attenuated polioviruses in human populations. Although this volume, prepared by an outstanding group of contributors, affords an excellent treatment of the various aspects of poliovirus infection, it was published too early to permit inclusion of data on active immunization with formalinized poliovirus vaccine. Such a lack limits the usefulness of the monograph considerably, and places it in the pre-immunization era for persons working in public health. The work also lacks specific sections concerning pathogenesis, pathology, and virus infections producing illnesses resembling non-paralytic poliomyelitis. These would be helpful in the reader's efforts to relate the various sections to each other and to understand further the broad spectrum of poliomyelitis infection.

This book will be most useful for persons interested in the epidemiology and in the study of poliovirus infections with the newer tissue culture techniques. It will be less useful for those interested in currently accepted control measures.

PAUL F. WEHRLE

EXPERIMENTAL METHODS FOR THE EVALUATION OF DRUGS IN VARIOUS DISEASE STATES. *Ann. N. Y. Acad. Sci., Vol. 64, Art. 4.*

Edited by Otto v. St. Whitelock; associate editor, Franklin N. Furness; consulting editor, Bradford N. Craver; 42 contributors. New York Academy of Sciences, New York. $4.00 (paper). Pp. 463–732; ill. 1956.

The conference on which this monograph is based considered experimental techniques employed in pharmacological research for selecting types of activity that may have clinical usefulness. The papers, by 41 authors, cover 5 areas: Collagen Diseases, Angina Pectoris, Cardiac Arrhythmias, Atherosclerosis, and Disorders of the Central Nervous System. Each paper is well documented with a selected bibliography.

C. JELLEFF CARR

ANTIBIOTICS *Annual 1954–1955. Proceedings of the Second Annual Symposium on Antibiotics sponsored by U. S. Department of Health, Education and Welfare, Food and Drug Administration, Division of Antibiotics; in collaboration with the Journal of Antibiotics & Chemotherapy, October 25–29, 1954, Washington.*

Edited by Henry Welch and Felix Marti-Ibañez; chair-

man, Henry Welch. Medical Encyclopedia, New York. $10.00. x + 1154 pp. + 1 pl.; text ill. 1955.

This volume contains 172 papers presented at this symposium. Since so much new material accumulates within a year in this rapidly growing field, these conferences have become annual affairs. Those who are interested in keeping abreast of the literature on antibiotics are greatly indebted to the editors for making these papers available in this manner.

C. JELLEFF CARR

DICTIONARY OF POISONS.

By Ibert and Eleanor Mellan. Philosophical Library, New York. $4.75. 150 pp. 1956.

This book represents a contradiction. It is recommended to everyone who may be called upon to render first aid to a victim of poisoning. It is said to be written in down-to-earth language that everyone can understand. Yet the volume contains an alphabetical listing and description of poisons which include such items as dichloroethyl ether, quaternary ammonium salts, and 2,4,5-trichlorophenoxyacetic acid, recognition of which would be difficult for the average layman. There are better books than this on the emergency treatment of poisoning for the home medicine chest.

C. JELLEFF CARR

PSYCHOLOGY AND ANIMAL BEHAVIOR

LEARNING AND INSTINCT IN ANIMALS.

By W. H. Thorpe. Harvard University Press, Cambridge. $10.00. viii + 493 pp. + 9 pl.; text ill. 1956.

The author states that one of the principal purposes of his book is to point out to psychologists and learning theorists, on the one hand, and to zoologists and physiologists on the other, how each is dependent, or ought to be, upon the work and viewpoint of the other. From this point of view the book is clearly a major contribution to its special field of learning. For many years, especially in America, there has been a tendency among psychologists and students of learning to confine all of their attention to men and laboratory animals, to the exclusion of other forms of life. Interest in invertebrate animals and in the so-called wild animals has been conspicuously lacking. On the other hand, comparative physiologists and zoologists interested in behavior have been ignorant, for the most part, of the contributions of psychologists. One of the great merits of the present book is that it successfully bridges the gap between disciplines. "To this end it has been thought necessary to provide a critical discussion of certain crucial parts of both instinct-theory and learning-theory and to give a detailed survey of the learning abilities of the main animal groups considered in relation to their instinctive equipment and the problems which they meet under natural conditions." The theoretical and philosophical implications of modern behavior study are in part considered in Part I. Problems of directiveness and purposiveness and the nature of drive are discussed in this section. Part II deals with types of learning and their interrelations. Part III relates the learning abilities of animals to the degree of development and organization of their instinctive actions and to their behavior in nature. The factual information which this book brings together, and the syntheses which it attempts, make it required reading for anyone interested in the problem of learning, even though he may not be in full agreement with all of the ideas expressed.

V. G. DETHIER

PERCEPTION AND THE REPRESENTATIVE DESIGN OF PSYCHOLOGICAL EXPERIMENTS.

By Egon Brunswik. University of California Press, Berkeley and Los Angeles. $5.00. xii + 154 pp. + 1 pl.; text ill. 1956.

This book has two main sections. The first is concerned with the author's notions about representative experimental design. The second shows how this kind of experimental design can be applied to the study of perception. Much of the content of the book has appeared elsewhere in individual monographs and other publications.

Brunswik argues that we should not adhere to the systematic, controlled, single-variable type of experimentation in psychology, but should aim rather to use experiments which sample widely from objects in the real world. He wants a multidimensional, real-world, psychophysics. Some of the experiments he has performed with this technique are clever and extremely productive. The procedure could well be applied to other types of psychological experimentation.

In the second section of the book, Brunswik is concerned with the cues for perception. Although he does not evolve a theory of perception in the usual sense of the word, he does make some astute observations about the way we perceive, especially as regards the perceptual constancies.

This is a research monograph, not a textbook. Unfortunately, the author has such an exceedingly intricate style of writing that it takes an extraordinary amount of effort to read even a few pages of the text. This is indeed unfortunate, for it probably means that his book will not receive the attention it justly deserves.

A. CHAPANIS

THE GROWTH AND STRUCTURE OF MOTIVES. *Psychological Studies in the Theory of Action.*

By James Olds. The Free Press, Glencoe. $5.00. 277 pp.; ill. 1956.

The material of this book is based largely on work done at the Harvard Laboratory of Social Relations. In it, the author attempts to give an experimental and theoretical explanation of the learning of motives, the effects of rewards on behavior, the establishment of (learned) object systems within the control apparatus, and the establishment of other action-control structures.

Psychology, more than any science, is rich with a plethora of "common sense" data, and suffers therefrom. What to do about this rich burden? One may agree with Skinner that theory is unnecessary to explain well-established psychological correlates; or one may see theory simply as giving demonstrable examples of such correlates; or beyond that, as furnishing a means of understanding things not at first envisaged in the establishment of the theory.

The author first presents the accepted facts of stimulus-response (S-R) in terms of "classical" and "instrumental" conditioning. Then he proceeds to the formulation of a limited theory of reward, and stresses three points.

(1) The *terminal* function of stimuli is added to the instigating function.

(2) The *directionality* of the associational bond between the "assemblies" permits dispensing with a law of effect in learning. The associational relation describes the transmission of environmental stimulation forward, but only for a backward flow of motivational facilitation. In this respect, Olds goes beyond Hebb, who had suggested that a backward flow could occur. It *must* be backward in all motivated facilitation, according to Olds. [Incidentally, this has no known physiological grounding.]

(3) It may be presumed that every "assembly" is a motivator. "Thus, one is never in the position of having to show how the laws of motivational learning implant desire where it never grew before. Wherever there is an idea, a perception, wherever an organism shows by an adaptive response that a stimulus has meaning, there is some intrinsic motivation." All learning requires reinforcement.

The author next proceeds to show that the elemental structure of S-R psychology can be viewed as an action system, in the sense that Parsons, Bales, and Shils used the term in connection with societal analysis. S-R structure is composed of three units—stimulus, response, and outcome—operating in four phases of its cycle: (1) the integrative adaptive, (2) the instrumental adaptive, (3) the gratificatory and (4) the latent phases. The antecedent concept plays the integrative-adaptive role, the action concept the instrumental-adaptive role, and the outcome concept plays the gratificatory role. The author sees the elemental action system as likewise having four measurable dimensions: a latent pattern force, a level of integration, a level of adaption, and a level of gratification. He achieves a psychological interpretation of the action system theories. Further, he attempts to extrapolate from the simpler S-R psychology to the more complex behavioral aspects. The useful concepts here developed show:

(1) Two dimensions of repeating experience:
  (a) a structure built up of short-run, low-contingency repetitions, called "object systems"; and
  (b) a structure built up of long-run, high-contingency repetitions, called "temporal systems";
(2) Two kinds of motivation:
  (a) goal-determined in an object system;
  (b) curiosity, when object system is not engaged;
(3) Single and double contingencies;
(4) The social object.

Object systems are, for the most part, environmentally determined. To record object systems requires a recording system which mirrors the rigidity between a large number of aspects and appearances, and in which order of sequence does not count heavily. In temporal systems, by contrast, some sort of long-run recording principle is necessary, and one which distinguishes between different long sequences, even when some of the same items appear in them. Both systems are operative in interpersonal relations (the social object).

Finally, Olds erects a complex theory of object systems, and for the temporal system resorts to the analogy of the wire recorder as a model of the association system of the brain. In this last item he deliberately returns to the fringes of electroneurophysiology, because he seems to believe that further clarification of psychology will come from multiple observations as exemplified in recent experiments from Hebb's laboratory, where electroencephalograms are recorded on rats which are running mazes or solving problems. His is an appeal to the communications engineer of the future to come to the rescue of psychology.

WENDELL MUNCIE

PHYSICS, PSYCHOLOGY AND MEDICINE. *A Methodological Essay.*

By J. H. Woodger. Cambridge University Press, London; [Cambridge University Press, New York.] $1.75. x + 146 pp.; ill. 1956.

This little book is an expansion of some material from the author's lectures to senior students of the physiology department of the Middlesex Hospital Medical School. It deals with a controversial subject, namely, the need for more psychological instruction in the basic medical curriculum.

The author, in an effort to present the matter in an impartial manner, and in order to keep down heat and afford more light, resorts to the theory of relations. By

the use of diagram and syllogism he shows conclusively that psychological facts can be dealt with only by methods peculiar to psychology, and that efforts to deal with them by the methods employed by physics cannot do justice to the facts. He indicates that his readers will regard his efforts as resulting in platitudes or heresies.

In America we have arrived at the same results as Woodger by the simple process of postulating them—backed by Adolf Meyer's philosophy of psychobiology—and then allowing the results to justify the postulates. Conventional medical circles must be more resistant in Great Britain, but it is hard to see how they could resist Woodger's logical demonstrations, if they but read them. He makes the interesting suggestion that it would be better if new theories were eagerly received, and skepticism withheld, rather than (as is the current practice) to have them viewed skeptically at the beginning, with acceptance slow to come. A good suggestion, but one which runs counter to all the well-known facts of habit formation! This is a worthy medical document, to be read with profit by all doubters.

WENDELL MUNCIE

BEHAVIOR THEORY AND SOCIAL SCIENCE.

By Frank A. Logan, David L. Olmsted, Burton S. Rosner, Richard D. Schwartz, and Carl M. Stevens. Published for The Institute of Human Relations by Yale University Press, New Haven; Geoffrey Cumberlege, Oxford University Press, London. $3.00. x + 188 pp. 1955.

This book is an interdisciplinary effort on the part of representatives of anthropology, economics, linguistics, psychology, and sociology to explore the methodological and theoretical barriers to the development of a comprehensive analysis of human behavior. The authors concentrated their attention on the use of modern psychological principles of individual behavior, specifically the S-R behavior system of Hull and his colleagues for the purpose of predicting human social phenomena. The choice of an S-R framework was made because it seemed to provide the least common denominator for the disciplines, and Hull's system was chosen because it is an attempt at a comprehensive account of behavior, and his theory has been applied to several social sciences. As might be supposed, the authors do not come up with any new comprehensive theory because the facts available today do not permit this. Indeed, the various authors disagree among themselves on the feasibility of constructing such a theory in the foreseeable future. Considering the matter of the construction of theory, they conclude that postulates should be as few as possible, consistent with each other, and sufficient to make possible the deduction of theorems corresponding operationally to all relevant data. In fact, however, theories that attempt to predict natural phenomena generally fall short of this ideal. There follows a general description of the Hullian theory generally represented by the equation S—s—sEr—r → R. They conclude that the intervening variables in such a formula are constructs that may not be explicitly related to any physiological events. Concerning the quantification factors, they conclude that "theory can never be stated more exactly than the empirical generalizations upon which it is based." They discuss the definition and measurement of responses, and the consistency of behavior. They note four different methods of defining responses, as used by social scientists, based on: (1) movement of the organism; (2) change in a piece of apparatus; (3) the effect, presumed, on some organism other than the one being categorized; and (4) the presumed internal state of the organism as "perceived" by the observer. These methods may be combined. Hull foreshadowed some combinations of "movement" and "apparatus" methods, but the authors see little hope in such a development for social science usage.

In the chapter on stimuli, they discuss stimulus equivalence, motivation, and reinforcement. Motives have been distinguished on the basis of the terminal responses produced but, in the discussion of motivation, no mention has been made of the interesting concept of Olds that motivation derives exclusively from the goal. Concerning reinforcement, the authors assume that forgetting is not a passive process due solely to the lapse of time since learning. They consider it more likely that forgetting depends on interference between old and new responses. Behavior patterns may be lost through three processes: (1) through the development of new responses which are incompatible with older ones; (2) through lack of reinforcement; and (3) through the process of "fatigue" (Sherrington), similar to Hull's idea of reactive inhibition. Hull attributes the extinction of responses from lack of reinforcement to cumulative, conditioned inhibition. His theory runs into trouble over the well-known fact of the increased rate of relearning after a period of non-reinforcement. The authors conclude that this is because he *deduced* this inhibition as a competing non-responding habit, and because of his idea of the permanence of habits. If he had only *postulated* the inhibition, it need not have been endowed with the properties he ascribed to habits.

There follows a chapter on verbal language as learned behavior, and on the complications inherent for the theory in problem-solving and in implicit behavior antecedent to language. A chapter on "free behavior" concerns itself with behavior not strictly reducible to experimental procedure, essentially the normal, spontaneous social behavior of the human being, alone or in the aggregate (Meyer's "experiment of nature"). The authors suggest that the S-R model needs to be modi-

fied or replaced by an analysis of "comparative statics," based on the assumption of behavioral equilibrium. They suggest three models as offering clues to an experimental analysis of such free behavior. Social interaction is approached likewise from the paradigm of individual behavior. The capacity for one individual to lend support to another is of great importance for their analysis. They conclude this most interesting book by asserting that Hullian concepts furnish a 'starting point for interdisciplinary cooperation, but will require extensive revision to be really fruitful.

WENDELL MUNCIE

GROUP PROCESSES. *Transactions of the Second Conference, October 9, 10, 11, and 12, 1955, Princeton, N. J. Edited by Bertram Schaffner. The Josiah Macy, Jr. Foundation, New York.* $3.50. 255 pp.; ill. 1956.

This book is one of more than twenty reports of conference groups; each group meets for at least two days annually over a period of 5 or more years. The meetings are limited to 25 participants (members and guests). The goal is "the exchange of ideas and the stimulation of creation." The conference program has been properly viewed by the Foundation as "an experiment in communication in which there is room for improvement and need for frequent re-appraisal."

The volume begins with a brief biographical sketch of each of the participants. The topics include Sladen's authoritative study of Social Structure among the Penguins; Blauvelt's excellent account of Neonate-Mother Relationship in Goat and Man; Birdwhistell's concise Kinesic Analyses of Filmed Behavior in Children; and Bateson's The Message, This is Play, a study of the cues and social factors in this type of communication. Each session is followed by an interchange, and selected references are included under each topic.

I am personally impressed with the experimental nature of this type of interdisciplinary approach. The book presents many of the difficulties which hinder effective communication. One can appreciate the feeling expressed by one of the guests, J. D. Frank, when he "wondered out loud (during the First Conference) what a man interested in group therapy with human beings could derive from material about fighting fish, sea gulls and things of that sort." During the Second Conference, Frank stated that "it turned out to be an extremely profitable and exciting experience."

This type of conference, with its spontaneous interchange of ideas, encourages an increased regard for the other investigator's personality and methods. The volume will interest all students of group processes and those who are interested in learning more about social structure among animals.

JACOB H. CONN

HYPNODYNAMIC PSYCHOLOGY. *An Integrative Approach to the Behavior Sciences. Edited by Milton V. Kline; foreword by Roy M. Dorcus. The Julian Press, New York.* $6.00. xii + 367 pp.; ill. 1955.

There has been no major attempt to bring together the available experimental data of hypnosis into a systematic whole since Clark Hull published hrs findings twenty years ago. *Hypnodynamic Psychology* is an attempt to accomplish such an integration, and is a "reflection of the status of hypnosis in contemporary psychology and the allied behavior sciences." It includes "the significant contributions not only to medical and psychological therapy, but also to experimental and theoretical psychology, neurophysiology, social psychology and the broad field of psychodynamics." Such an ambitious project must fall short of some of its goals, but the overall result is very commendable. The topics, for the most part, are very well covered and are treated as belonging to a biosocial, systematic framework.

Each of the six contributing authors is an expert in his special field. The section dealing with the social aspects of hypnosis by S. Glasner is very well written and presents an effective discussion of learning through hypnosis and the author's data concerning the modification of social attitudes. The moot question whether a subject who is under the influence of hypnosis can behave in an antisocial manner is answered affirmatively, provided that the subject is made to perceive his actions as occurring in a context in which they are not considered as being antisocial.

The major portion of the book (130 pages) is devoted "to the contributions and the relationship of scientific hypnosis to the theoretical and conceptual aspects of psychotherapy." The motivating factors involved in resistance to the induction of hypnosis, therapeutic change, the techniques of scene-visualization projective methods, word association, and age alterations (regression and progression) are well described and carefully evaluated by the editor, M. V. Kline.

The section on Basic Psychological Principles and Hypnosis, by H. Guze, is an erudite discussion of sensory basis, perception, the problems of conditioning and learning, and unconscious processes associated with the hypnotic trance state.

F. L. Marcuse is the author of the fourth chapter, which is a concise and authoritative review of the history and "the maze of discrepant and contradictory" data of Animal Hypnosis and Psychology. Marcuse wisely concludes that the similarities between animal hypnosis and human hypnosis have been emphasized and that the significant differences have been ignored.

The section on Experimental Psychopathology, by A. Sweetland, presents a variety of experimental procedures and an excellent critical summary of experimental design for hypnotic investigation.

The last chapter, which is by A. Weitzenhoffer, provides a concise but inclusive description of the

physical, psychic, and mixed or physicopsychic methods which have been used in the induction of the trance state. The author stresses the fact that "hypnosis is a psychological process and the effective hypnotist is an effective psychologist. The most effective method of inducing the trance aims at evoking suggestibility on all of its dimensions to the fullest extent . . . and . . . this involves using a number of processes. . . ."

A comprehensive, authoritative subject index is included. The book can be highly recommended as an introduction to the study of the theory and practice of modern hypnosis.

JACOB H. CONN

PATTERNS OF MOTHERING. *Maternal Influence During Infancy.*

By Sylvia Brody; introduction by Rene A. Spitz. International Universities Press, New York. $7.50. 446 pp.; ill. 1956.

There never has been a "psychoanalytically inspired" book on the topic of mother-infant relationships with as much detailed observation as is to be found in Brody's book. It is psychoanalytic in theory, empathic in feeling, and comprehensive in scope. The literature on feeding behavior in various cultures, the genesis of motherliness, and infant growth are included, as well as detailed reports and quantitative evaluations of the reciprocal influence of 32 mothers and their babies at four age levels (4, 12, 20, and 28 weeks).

The book does not rest entirely upon the premise that the infant's destiny is derived principally from maternal attitudes. Most students of child behavior would agree that Freud's oral-anal theory oversimplifies matters, and that the infant's inner awareness and the factors influencing personal growth have a much greater complexity than is embraced by any of our current explanations of personality development. The author is very much aware that a "mother's behavior is determined by real circumstances, character structure, personal values and cultural standards," and concludes that "infants by virtue of their inborn demands will call out particular reactions in their mothers," and "that independent psychological factors in the behavior of mothers can be observed to operate from the first weeks of the infant's life." The theoretical section will be difficult for the average reader. The book can be recommended to all students of child behavior as an excellent study of parent-child relationships in a systematic, psychoanalytic context.

JACOB H. CONN

TRUANTS FROM LIFE. *The Rehabilitation of Emotionally Disturbed Children.*

By Bruno Bettelheim. The Free Press, Glencoe. $6.00. xvi + 511 pp. + 8 pl.; text ill. 1955.

The author of *Love is Not Enough* has now written a detailed account of the histories of four children, their personality problems, and the nature of the treatment given them by the members of the staff of the Sonia Shankman Orthogenic School which is a part of the University of Chicago. There is a follow-up of these children after an interval of three years. Bettelheim repeatedly calls attention to the fact that the staff works with only the most disturbed children, those who from an early age have been totally unable to function in society.

There is first presented a detailed description of the school and how it is organized. The histories of the four children (one of which histories originally contained several thousand pages) include many episodes of aggression, anxiety, anality, masochism, problems of identification, and psychoanalytic and psychotherapeutic procedures.

A follow-up study of 31 children treated at the school disclosed that 15 were "rehabilitated," 11 were "much improved," three "somewhat improved," and 2 were described as presenting "no lasting improvement."

The book is a tribute to the members of the staff, 17 of whom have been at the school for more than two years. These therapists experience "hate, neglect, abuse" and yet must be able to remain "positively attached" to the patient. It is even more difficult when the staff member becomes "the target of negative feelings" and "an object of displeasure," and yet must continue to help the child to care for another staff member who enjoys both being loved and the pleasure of "carrying forward the therapeutic work." Obviously these situations create interstaff difficulties which must be overcome if the child is to be treated successfully. One cannot help being impressed by the degree of self-renunciation demanded from the various staff members, when they try to help these seriously mentally disorganized children (who remain at the school for a median stay of 3 years). The results of this teamwork are revealed in a statistical table. An appendix evaluates the patients' families and mentions that the tuition is $4,500 yearly. Many of the children receive partial "scholarships."

Truants from Life is the best possible example of the need and value of residential treatment. The book vividly demonstrates that although "love may not be enough," it certainly is the basic ingredient in the therapeutic formula.

JACOB H. CONN

ALCOHOLISM, *Its Psychology and Cure.*

By Frederick B. Rea. Philosophical Library, New York. $3.50. 143 pp. 1956.

The author of this book is not identified further than as a person who found himself invited to help in the formation of an Alcoholics Anonymous group. The book has been written after four years of working with that group. Rea presents an excellent statement of the alcoholic problem from every standpoint, looking upon it as an addiction with physical, psychological, and spiritual aspects. He discusses the various aversion treatments. Particularly helpful are the chapters on the significance of conversion (essentially, that point at which the patient's defenses are broken down and he decides to forsake his drinking and lead a new life); the chapter on Alcoholics Anonymous; and the chapter on the pastor and the alcoholic.

I believe that Rea has produced a small volume which is very worthwhile, one from which physicians, psychiatrists, social workers, and ministers can receive much sound instruction. This book should be particularly useful to ministers, in that it seeks a true resolution of the dilemma of sin versus illness in the problem of alcoholism.

WENDELL MUNCIE

TECHNIQUES FOR THE STUDY OF BEHAVIORAL EFFECTS OF DRUGS. *Ann. N. Y. Acad. Sci., Vol. 65, Art. 4. Edited by Otto v. St. Whitelock; associate editor, Franklin N. Furness; consulting editor, Peter B. Dews; 12 contributors. New York Academy of Sciences, New York.* $3.00 (paper). Pp. 247–356; ill. 1956.

The 8 papers which comprise this volume describe quantitative studies that have been made upon animals and man in an effort to observe behavioral patterns that might lend themselves to drug evaluation. With the pharmaceutical industry spawning new ataraxic drugs at a bewildering rate, it is imperative that the tools of the behavioral sciences be sharpened to evaluate these new agents. The techniques outlined in some detail in these papers include a study of behavioral patterns in cats; conditioned fear or anxiety in rats; positive reinforcement performance schedules in pigeons; differential reinforcement schedules on behavior patterns in rats; characteristics of behavior maintained by complex schedules of intermittent, positive reinforcement in pigeons; studies in motivation in rats using a variety of measures (hunger, thirst, fear, etc.); discriminating behavior in the pigeon; and description and analysis of mood in man.

C. JELLEFF CARR

HUMAN BIOLOGY

MAN'S NATURE AND NATURE'S MAN. *The Ecology of Human Communities. By Lee R. Dice. The University of Michigan Press, Ann Arbor.* $5.00. viii + 329 pp. 1955.

Professor Dice, whose *Natural Communities* is a pillar of the ecological literature, in the present book extends his thoughts to a subject so foreboding in its complexity that it has almost wholly eluded serious ecological analysis. This is the human community, tarnished crown of primate evolution. He seeks to itemize regulative processes effective in the human community, and to demonstrate its interrelationships with the biological and physical environment. Obviously not much more than an outline can be attempted; the subject is too large for one author and, as he admits, "Practical methods for describing and measuring the various ecologic features of human communities in quantitative terms are still largely lacking, especially for the complex interrelations within an industrial community." It is not unexpected, therefore, that this is a superficial book. This does not mean it should not be read; it does, at least in most instances, put man in an uninflated, reasonable perspective and show that a biologically oriented analysis of his communities is desirable and ultimately possible.

For the present, there seem to be areas of human activity which the ecologist is not well qualified to explore. Morality and moral codes assuredly are regulatory phenomena in the ecological sense; they tend to favor behavior beneficial to community survival. But Dice's foray into the subject illuminates little and would even suggest that he has interpreted nature to fit his philosophy. He rejects, without a hearing, mechanistic concepts of life, and subsequently embraces a highly mechanistic moral philosophy. Again, in his consideration of regulatory mechanisms we find an interesting example of ecologic romanticism. He writes, "At a higher level of integration the natural ecologic community . . . operates as an essentially democratic system." Predator and prey, senator and citizen!

In short, we have here a commendable effort which suffers from necessary superficiality and sometimes from an unnecessary lack of objectivity.

JAMES F. CASE

MAN, CULTURE, AND SOCIETY. *Edited by Harry L. Shapiro; 17 contributors. Oxford University Press, New York.* $7.50. xii + 380 pp. + 13 pl.; text ill. 1956.

As the title suggests, this book deals with the field of anthropology. There are 16 chapters and as many contributors, each of them of senior scholarship. This selection of authors makes possible an incisive, if brief, exposition of topics. One chapter, by the editor, is devoted to man's presumed origin and his early physical traits. Five chapters are concerned with the prehistoric conditions; five, with culture; two, with social life; one,

with religion; one, with economics; and a final chapter, by Robert Redfield, tells us How Human Society Operates. In some chapters one could wish for more illustration and detail, and in some, one could do with less. In some instances, when there are no discoverable crucial data, the very lack of them inspires speculation. What gave rise to the races? What traits distinguished the social and mental life of prehistoric man? These, however, are not unique ventures.

A gem, no less, is Leslie Spier's Inventions and Human Society; and many who read the final chapter will derive profit and pleasure. None of the contributions is dull, and none is unrewarding.

WILSON D. WALLIS

AGEING IN INDUSTRY. *An Inquiry, Based on Figures Derived from Census Reports, into the Problem of Ageing under the Conditions of Modern Industry.*

By F. LeGros Clark and Agnes C. Dunne. Philosophical Library, New York. $7.50. x + 146 pp. 1956.

This book rests upon a major fact, a major assumption, and quite a few hypotheses. The data are from England. The fact is that "we are an ageing population." The assumption is that "there will remain a high demand for labour and a reasonable appreciation of the value of ageing men in industry." The hypotheses are resident in the statistical treatment of the data. The aims of this book, pertinent to a U. S. culture pattern as well, are to make "a survey of modern industry from the viewpoint of its older operatives" and an attempt to determine "what numbers of workers are physically able to continue in their various occupations beyond their mid sixties."

The data are from tables of age and occupation in the British census reports for 1921, 1931, and 1951. A total of 32 occupations are studied. In 1951, 4,004,700 persons, or 25.6% of the 15,662,220 occupied males, were engaged in these occupations. Further, in these 32 groups there were 174,000 employed men over 65 years of age, comprising 25% of the total 695,300 men past 65 who were gainfully employed. The representation seems adequate.

Here are some very pertinent facts: (1) In 1931, there were 1,424,800 males of 65-plus; in 1951, there were 2,174,800, a gain of 749,995, or 52.6%. (2) In 1931, employed males over 65 numbered 682,779; in 1951, there were 695,300, a gain of only 12,251, or 1.8%. (3) In 1931, 47.9% of males over 65 were occupied, and in 1951, only 32.0% were occupied. (4) In 1931, males 65-plus were 6.64% of the total male population; in 1951, they were 9.28%. (5) In 1931, occupied males 65-plus were 3.18% of the total male population; in 1951, they were 2.79%. This sort of total population versus occupied 65-plus dislocation demands analysis.

The authors of *Ageing in Industry* set up what they term three "exercises:" (1) to follow members of decennial age-groups, or *cohorts*, in each occupation for the period of their employment; (2) to relate different age-groups within each occupation at successive census dates; (3) to analyze for each occupation the changes in age-structure, 1931–1951. The criteria for selection of occupations to be studied were as follows: (1) most workers must have been settled in that occupation by their early thirties and must have remained in it thereafter; (2) the occupation had to be clearly definable; (3) no radical changes within the occupation should have occurred in the past 30 years. On these bases the following 32 occupations were studied: farmers, agricultural workers, foresters and woodmen, coal miners (hewers and getters, others below ground, surface workers), brick- and pottery-makers, makers of glass, foundry workers (moulders and core-makers), smiths and forgemen, platers, riveters, plumbers, watch- and clock-makers, workers in precious metals, welders, construction engineers, makers of boots and shoes, makers of tobacco, cabinet-makers, carpenters, paper-makers, compositors, makers of musical instruments, bricklayers, plasterers, signalmen, train and trolley-bus drivers, drivers of self-propelled vehicles, bus and tram conductors, forgemen and tugmen, dockers, shop assistants, and warehousemen.

The bulk of this book consists, as one might expect, of the application of each of the three "exercises" to each of the 32 occupations. In pursuance of this plan, Exercise 2 offers two very important ratios (Tables 1 and 2). The first ratio is, "Men aged 55–64 : men aged 35–64," calculated for 1921, 1931, and 1951. There is no consistent pattern, save a higher ratio in 1931; the 1921 and 1951 ratios are fairly even. The range (1951 only) is 9.25 for bus and tram conductors to 33.25 for makers of musical instruments. The second ratio is, "Men aged 65 and over : men aged 35–64." Here the range is 1.0 for tram and trolley-bus drivers to 31.0 for makers of musical instruments. It is concluded for these data that, "while there is little difference among the occupations for men who are only approaching the age of 65, from about the age of 65 onwards the contrasts between one job and another become marked." It is felt that the contrast is "in the very nature of the jobs themselves."

The final equation in this report is what is termed a job *survival rate*. It is an answer to the question, "What proportion of the men who reach their mid-sixties in a given job are physically capable of remaining on the same job into their late sixties or even in some cases beyond?" The answer, in the form of percentage survival rates, is given on pp. 140–41, which should be consulted. Old established crafts (watch-makers, etc.) rate highest, 75–85%; while coal-face workers rate lowest, 5–15%. It is held that "the capacity of men to continue beyond their mid-sixties depends mainly (and

for the general run of men) upon the actual jobs they have to do."

This is a cautious, conservative, tightly written book. It is a distinct contribution to the solution of a problem basic to Occidental culture: the socio-economics of the later years of life. Public health programs, social and "socialized" legislation must take notice of the problem. Here is more than a beginning—here are guide-posts!

W. M. KROGMAN

TABOO.

By Franz Steiner; preface by E. E. Evans-Pritchard. Philosophical Library, New York. $4.75. 154 pp. 1956.

There are at least three other books and scores of articles and chapters devoted to taboo, but none has an approach and treatment comparable to those of Steiner. He traces the use of the word from its adoption in the latter half of the eighteenth century, after contacts with Polynesia, to contemporary times, and supplies a critical analysis of various interpretations of the practice of taboo, notably those of Frazer, Marett, Wundt, Freud, Radcliffe-Brown, and Evans-Pritchard. The author concludes that "taboo is an element in all those situations in which attitudes to values are expressed in terms of danger behaviour, and . . . all the things discussed under the heading of taboo cannot be seen in terms of a single problem" (p. 147).

WILSON D. WALLIS

CHILD DEVELOPMENT. *Third Edition.*

By Elizabeth B. Hurlock. McGraw-Hill Book Company, New York, Toronto, and London. $6.00. xvi + 703 pp.; ill. 1956.

The publication of a third edition of a book usually indicates the success of an idea. Characteristic of Elizabeth Hurlock's book are its clarity, the presentation of what is established as fact, and the avoidance of fanciful theorizing. The author has completely rewritten the original text. Graphs have replaced tables, and much new material has been added. The emphasis is "upon cultural influences and the role they play in determining the pattern of the child's development."

The result is a well-written, objective, carefully edited account of what is of value to the college student in the field of child development. There are 15 chapters (one for each week of the usual college semester). The areas of physical, mental, emotional, and social development are covered in sufficient detail. An expanded bibliography and adequate subject and author indexes are included. The book can be recommended as a standard textbook for college students.

JACOB H. CONN

THE PHYSICAL GROWTH OF CHILDREN: AN APPRAISAL OF STUDIES 1950–1958. *Monogr. Soc. Res. Child Develop., Vol. XX, Ser. No. 60, No. 1, 1955.*

By Wilton Marion Krogman. Child Development Publications, Lafayette. $2.50 (paper). iii + 91 pp.; ill. 1956.

The author's review of available literature regarding the physical growth of children for the period 1950–1955 makes this material more accessible for persons interested in the field.

The monograph is divided into three portions. The first is a brief digest of the available data published during the stated period. Specific areas which are considered include height and weight, ethnic differences in growth, general body growth, body build and composition, bone growth, circumpubertal growth, and exogenous factors in growth. There are brief specific comments regarding the content of the various publications mentioned, and this section contains numerous tables and graphs.

The second portion consists of the author's brief evaluation of the types of studies reviewed and of general progress in the field during the 5-year period studied. The third section is a comprehensive bibliography of 222 books and articles published in this field during the period 1950–1955.

A careful and thorough review of the literature in this growing field of study and a clear indication of some of the deficiencies inherent in traditional somatometry appear to have been made by the author. The work represents a positive contribution most useful to persons interested in the growth and development of children, but it will also be helpful to those working in related fields.

PAUL F. WEHRLE

THE PHYSICAL ANTHROPOLOGY OF IRELAND. *Papers of the Peabody Museum of Archaeology and Ethnology, Harvard Univ., Vol. XXX, Nos. 1 and 2.*

By Earnest A. Hooton and C. Wesley Dupertuis; with a section on The West Coast Irish Females by Helen Dawson. Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge. $10.00 (paper); $13.00 (cloth). (1) xx + 304 pp.; ill. (2) tables + 47 pl. 1955.

One is tempted to observe, "Once upon a time there were two Irishmen, Patricia and Michael—now there are millions!" Who are they? Where'd they come from?

This study offers some answers, provided basic procedures and concepts are accepted. The sampling method seems to have been fairly adequate. Dupertuis measured 10,000 males, Dawson 2,000 females. Some 426 towns and villages in 46 counties were covered. Measurements, morphological observations, and various social data (religion, education, language, occupation, etc.) were gathered. In substance, therefore, this is a bio-social population analysis.

The first volume is divided into four parts. Part I is entitled Catholics by County Subgroups. This group is divided and discussed by counties and by groups of counties, the latter termed "ethnographical regions." Part II is a Comparison of Catholics and Protestants. Part III brings us to the substance of the report, a racial breakdown of the study, Morphological (Subracial) Types. The basic criteria center around hair- and eye-color and cephalic index, with nasal index and stature brought in as corollaries (corroborative). The technic here is a direct carry-over of the race-concept method developed by Hooton in his criminal-type study. A type emerges, more or less as a constellation or matrix, when the data are sorted by statistical routines. Clusters which are more or less distinct are tagged on the basis of an analogue, i.e., a statistical group is named because of its closeness to a previously identified or recognized racial entity. With this principle established in the thinking of the authors, a subracial classification of the Irish emerges: Nordic-Mediterranean, 28.9%, Keltic 25.3%, Dinaric 18.6%, Nordic-Alpine 18.4%, Predominantly Nordic, 6.8%, East Baltic, 1.1%, Pure Nordic 0.6%, Pure Mediterranean 0.3%.

The racial picture, for both the present and in terms of historical origins, is summed up by the authors as follows: "It is important to note, however, that in both Ireland and Wales the proportionately strongest morphological type is what we call Nordic Mediterranean—long-heads with dark hair and mixed eyes. This seems to be the fundamental type of the British Isles. It probably incorporates in both countries the bulk of the descendants of Palaeolithic settlers (present in Britain only), of the Mesolithic inhabitants, of the Neolithic and Megalithic peoples with some reinforcements from later comers" (p. 235). The reference to the Paleolithic settlers is only in terms of remote origin via an absorbed blending, for Hooton specifically challenges Coon's idea of "Paleolithic survivors" as a sort of re-emergence, or even persistence, analogous to geologic outliers representing differential erosion. There is, avers Hooton, no survivorship—only a basic element in an eventual amalgam.

There is one other concept worth noting. Because dark eyes and skin, with many pigmented moles, and wavy hair are more frequent in younger than in older population samples, the authors suspect a survival value of opposite traits. This smacks of Graves' "plus-potential survival value" of convex scapulae and dolichocephals. The idea is not a proved, nor yet even a demonstrable, one; for the entire study is cross-sectional, and direct age-sample comparability is impossible.

When all's said and done, one can but conclude that here is a remarkably thorough piece of work. The Irish, bless 'em, emerge as one of the best-known (anthropologically speaking) peoples of our time. Dawson, Dupertuis, and Hooton have produced a pilot-study that must be a guide to all further mass studies.

W. M. KROGMAN

PREHISTORIC SETTLEMENT PATTERNS IN THE NEW WORLD. *Viking Fund Pub. Anthropol., Number 23. Edited by Gordon R. Willey. Wenner-Gren Foundation for Anthropological Research, New York.* $5.00 (paper). viii + 202 pp. 1956.

Several scholars, specialists in the anthropology of the New World, have each contributed a short paper on New World prehistoric settlements. The regions include most of North America, Middle America, and much of South America and the Caribbean area. An endeavor is made, whenever possible, to link the prehistoric with the historic. There are also many endeavors, when it is impossible to do so, to reveal various non-material phases of the prehistoric—religious beliefs, social organization, magical practices, etc. One contributor frankly confesses that "the deductive use of analogy and extrapolation, employing, as ethnographic patterns within the area, the northern Algonkian tribes for the earlier cultures and the Iroquoian tribes primarily for the later, predisposes the writer to the delusions of circular reasoning and foibles of syllogistic logic" (p. 72). One doubts that syllogistic logic has foibles; but certainly users of it are not necessarily exempt from them. Having thus reassured us, the writer proceeds to tell us what nobody could conceivably know.

How can anyone know that a certain prehistoric group consisted of "small, semi-isolated, individualistic, and relatively unstable bands composed of kinsmen and congenial outsiders, under temporary chieftainship" (p. 79)? How can he know that "the greatest elaboration of many aspects of culture, including religious ideology, were reached . . . ," or that "a marked regression in magico-religious activities and in some probably related aspects of the material culture characterizes the succeeding stage" (p. 79)? Does looking through the crystal ball at the past allow more accuracy than looking through it at the future? Or may one merely be seeing through a glass darkly and imagining shapes whose reality, by the very nature of the case, can neither be proved nor disproved? Does the archeologist have any more need for "circular

reasoning" or any less need for "syllogistic logic" than another scientist?

WILSON D. WALLIS

FAMILY AND FERTILITY IN PUERTO RICO. *A Study of the Lower Income Group.*

By J. Mayone Stycos. Columbia University Press, New York. $6.00. xviii + 332 pp. 1955.

"The raw material for this book comes from lengthy interviews with 72 husbands of the lower-income class and their wives: 24 from three rural areas, 24 from an urban area, and 24 from three small towns" (pp. 23–24). Households were selected from a list including only houses valued at less than $250 by the Tax Assessment Bureau. From December, 1951, to March, 1952, Mr. Stycos interviewed these people, all of whom inhabited one section of the island. He has collected material pertinent to such topics as: Differential Status; Ideologies of the Sexes; Child-Rearing Practices; Courtship; Early Marriage and Consensual Union; Marital Relations; Attitudes toward Fertility; the Fertility Belief System; Attitudes toward Birth Control; Dynamics of Birth-Control Use; and Recommendations. A section on methodology, containing the forms used in interviews, appears in the book.

"In Puerto Rico . . . excessive population growth imperils the whole society." Birth-control methods are known to the poorer families and are practiced to some extent. But traditional ideas and attitudes hamper wide use of them. Making clinics physically more accessible to rural peoples is one of the author's recommendations for improving the conditions he found in Puerto Rico.

WILSON D. WALLIS

MANAGEMENT OF ADDICTIONS.

Edited by Edward Podolsky. Philosophical Library, New York. $7.50. xviii + 413 pp. 1955.

This book is comprised of 35 chapters by approximately twice as many contributors. It presents in detail about all there is to say concerning the problem of alcohol and drug addictions. The various chapters deal not only with the background of addictions in personality problems, environmental issues, and physical or physiological disorders, but also give in detail the numerous, present-day procedures of treatment followed in various situations. The presentation of treatment is concerned with symptomatic as well as with more basic treatment. As perhaps befits the relative importance of the two problems, 26 chapters are devoted to alcohol and but 9 to drugs. This book constitutes authoritative statements concerning the many present-day procedures in these fields, and can be highly recommended.

WENDELL MUNCIE

DICTIONARY OF ANTHROPOLOGY.

By Charles Winick. Philosophical Library, New York. $10.00. vii + 579 pp. 1956.

I do not know the approved method of reviewing a dictionary. One reads it through and finds much of interest, but may miss the plot. Here we start with *à dos rabattu. See Back, Battered,* followed by *à froid.* The closing item is *Zygomatic arch. See Arch, Zygomatic.* Phrases as well as single words are included, and cross-references are frequent. Some users, to be sure, would prefer a different manner of listing items in which more than one word is the entry. I imagine, for example, that one who wishes information about the zygomatic arch would not turn to the word *arch* for that information; for the physical anthropologist, the primary connotation would be under *zygoma.* In any event, search will be rewarded. For many terms there are subheadings. Thus the entry *family,* to which more than a column is devoted, is followed by entries on: *bilateral, biological, composite, conjugal, consanguineal, elementary,* and ten others. Under divination there is reference to "closely linked" topics, of which 45 are listed. Many important items receive a brief, encyclopedic treatment. For example, nearly a page is devoted to *horse.* The various human fossils listed under *Homo,* with a designating subtitle, receive brief accounts; yet *Homo neanderthalensis* receives more than two columns.

Many native names from various parts of the world are included, as are those of persons whose activities fall before or about the beginning of the present century: *Conze, Alexander; Cook, Captain James.* This dictionary will certainly be consulted by many persons, both professional anthropologists and others. In the selection and the treatment of topics there is much to admire and nothing to carp about. The author of the volume acknowledges indebtedness to many persons who have assisted in the compilation or editorial revision of the volume.

WILSON D. WALLIS

BIOMETRY

PROCEEDINGS OF THE THIRD BERKELEY SYMPOSIUM ON MATHEMATICAL STATISTICS AND PROBABILITY. VOLUME IV. CONTRIBUTIONS TO BIOLOGY AND PROBLEMS OF HEALTH. *Held at the Statistics Laboratory, Univ. of California, Dec. 1954, July and August, 1955.*

Edited by Jerzy Neyman. University of California

Press, Berkeley and Los Angeles. $5.75. x + 179 pp.; ill. 1956.

The first part of this volume consists of three papers on biology. First, Crow deals with the deterministic effects of selection and mutation on population fitness, and Kimura next deals with the stochastic processes that have arisen from the random sampling of gametes and from the random fluctuation of selection intensities from generation to generation. Kimura gives several distribution formulas for gene frequencies with specified initial frequencies at any given time. Dempster reviews and discusses three recently developed methods of analyzing the genotypic variance of a measurable character in inbred and panmictic populations. Neyman, Park, and Scott present a 3-year co-operative study of the "struggle for existence" between two species of flour beetles. Neyman approaches the competition problem as a Markoff process.

The second part of the volume consists of 6 papers on health and epidemics. M. S. Bartlett tries to organize a quantitative theory of epidemics, and warns against the danger of comparing small-scale experimental studies with deterministic models. Bharucha-Reid first formulates some stochastic models for the spread of epidemics, and then considers the problems of statistical inference. C. L. Chiang et al. discuss the procedure of multistage screening and the problem of longitudinal diagnosis. J. Cornfield obtains confidence limits for estimates of the relative risk of having a disease. He uses lung cancer and smoking data as examples. D. G. Kendall deals with deterministic and stochastic epidemics in closed populations. Finally, W. F. Taylor presents some actual problems involving contagion (accident and epidemic studies).

All 9 papers are "mathematical" and are addressed to specialists in that subject.

C. C. Li

Experimental Design. *Theory and Application. By Walter T. Federer. The Macmillan Company, New York.* $11.00. xxii + 544 + 47 pp.; ill. 1955.

Experimental Design and Its Statistical Basis. *By D. J. Finney. The University of Chicago Press, Chicago.* $4.50. xii + 169 pp.; ill. 1955.

These books on experimental design represent two extreme types of treatment of the subject. Finney's small book is an attempt to make the subject intelligible to students of biology, and is not intended to serve as a textbook. It is exceptionally well-written, and in limited space the author touches upon almost every major aspect of biological experimentation. The reader will find it a very inadequate "recipe book"; but the experimenter will find plenty of good advice in it concerning experimental strategy, especially in the last chapter on The Selection of a Design.

Federer's comprehensive book is almost a complete and classified manual on experimental designs. Most biology students except in agronomy or plant breeding probably do not need many of the designs in this book, such as cubic lattices. But those who do need them can find probably more of them explained and illustrated by examples herein than anywhere else. In Chapters 2 and 3 there are collected some recently developed statistical methods that cannot be found in older textbooks. The analysis of covariance (Chapter 16) has been treated in great detail. At the end of the book are an additional 47 pages of practical problems, with source references. This book will serve well as a standard reference work for research workers as well as students.

C. C. Li

DE OMNIBUS REBUS ET QUIBUSDAM ALIIS

The Foreseeable Future. *By George Thomson. Cambridge University Press, New York.* $2.50. viii + 166 pp. 1955.

When Sir George Thomson undertakes a look into the future, we might profitably follow his penetrating gaze. Like his father a Nobel laureate in physics, Sir George has no crystal ball, but uses instead his broad knowledge and understanding of past and present progress in science to foresee the problems man is almost certain to face in the future. Characterized by informality and a sense of humor, his writing is, as always, eminently readable. Along with Ernest Baldwin, he can be included among those select scientists who fully accomplish the feat of translating scientific information into delightful prose.

Thomson introduces seven scientific "principles of impotence" (such as action and reaction, uncertainty, exclusion) to stress that the future is not as likely to be based on mechanical ingenuity as to be circumscribed by the natural limitations of time and matter. These are principles of physics and chemistry, but biological progress is, of course, likewise governed by them. Throughout the work, Thomson constantly refers to basic ideas and demonstrates their relevance to the everyday problem at hand.

The future is not quite utopian; but it is also not hopeless if we will use some of our knowledge and good sense. The probable doubling of the earth's population within the next century will bring problems to the entire globe, but especially to those areas already overpopulated. Thomson considers questions of energy and power supply, possible improvements in basic materials, transportation and communication complexities ("the most serious problem in modern transport is . . . the rush-hour"), and the advisability of trying to control the weather. While biology is ad-

mittedly beyond his field of specialization, his excellent understanding of the contribution it may make to the future is shown in his discussions of food supply, controlled mutation, race relations, and—what he considers medicine's most pressing challenge—old age.

The future social consequences of increased leisure, of automation and the subsequent disappearance of routine work in factories and on farms, of the increased importance of education, and of the lack of adventure are considered with perspicuous insight. After a final foray into natural and artificial thought, Sir George concludes that man's brain has only begun to realize its potentiality and that, if it continues to improve, the limits of man's achievement are truly unforeseeable.

FRANK C. ERK

BLAKISTON'S NEW GOULD MEDICAL DICTIONARY. *Second Edition.*

Edited by Norman L. Hoerr and Arthur Osol. The Blakiston Division, McGraw-Hill Book Company, New York, Toronto, and London. $11.50. xxvi + 1463 pp. + 45 pl. 1956.

I can imagine no task quite so boring as the compilation of a dictionary, nor any task quite so necessary to a great diversity of people. The present volume, made up of 1463 pages and 45 plates, has the medical profession in mind, but the biologist should also find it a mine of information. It differs from the first edition (*Q.R.B.*, 25: 127. 1950) in having some 12,000 new terms added and some 8,000 changes made. The plates, both in color and in black-and-white, are superb in their treatment of various anatomical aspects of the human body. The reader will also find a most useful set of tables in the Appendix, dealing with the following subjects: arteries, bones, joints and ligaments, muscles, nerves, veins, blood constituents, chemical elements, enzymes, hormones, isotopes, medical signs and symbols, microorganisms pathogenic to man, monstrosities and anomalies, phobias, pregnancy, prescription writing, proteins, thermometric equivalents, vitamins, and weights and measures.

A spot check of approximately 100 words reveals few definitions with which one can take exception, although not all may be as inclusive or as incisive as one might wish.

C. P. SWANSON

THE QUARTERLY REVIEW OF BIOLOGY publishes critical reviews of recent researches in all of the special fields of biological science. The contribution should present a synthesis or digest of the researches and a critical evaluation of them. A mere synopsis of the literature without evaluation or synthesis is not desirable.

Theoretical papers are published occasionally, especially when such papers (1) include a critical synthesis of the literature bearing on the theory and (2) are likely to promote further research in a given field.

The article should be written in concise language, yet in sufficiently non-technical form as to be intelligible not only to specialists in other fields but to the general biologist as well. To this end the article should have a general introduction and a summary which enumerates one by one all of the principal facts and conclusions given in the paper. Interpretative diagrams and schemes are very desirable.

Material ordinarily taking the form of footnotes is set in small print and placed in the text and consequently should be written in a style so as to fit readily into the text. Acknowledgments are printed in the text in small type at the end of the article just preceding the List of Literature. Recent issues of the Quarterly should be examined for style as regards (1) section or subsection headings in the text, (2) literature citations in the text, and (3) List of Literature.

The subjects and authors of articles are selected by the Editors and members of the Advisory Board. Unsolicited articles which conform with the objectives of the Quarterly will be considered for publication.

A feature of the REVIEW is the section dealing with *New Biological Books*. In this department the book literature of different countries in the field of Biology is given comprehensive and critical attention.

The QUARTERLY REVIEW OF BIOLOGY is issued in March, June, September and December.

The reprint order blank accompanying galley proofs gives the cost of reprints.

Manuscripts may be sent to Dr. B. H. Willier, Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland.

Books for Review may be sent to Dr. H. B. Glass, Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland.

New subscriptions and renewals are entered to begin with the first issue of the current volume. Should any issue of the current volume be out of print at the time the subscription order is received, the pro-rata value of such numbers will be refunded to the subscriber.

Subscriptions should be renewed promptly—To avoid a break in your series, subscriptions should be renewed promptly. The publishers cannot guarantee to supply back issues on belated renewals.

Subscription price: United States, $7.50 ($6.50 to members of the A.I.B.S.). Countries within the Postal Union and foreign countries, $8.25; Canada, $7.75. Single copies will be supplied, when available, at the rate of $2.00 a copy, plus $.25 postage outside USA.

Claims for copies lost in the mails must be received within 30 days (domestic).

Change of address—Publisher must be notified 60 days in advance. Journals undeliverable because of incorrect address will be destroyed. Duplicates can be obtained (if available) from the publisher at the regular price of single issues.

THE AMERICAN INSTITUTE OF BIOLOGICAL SCIENCES

2000 P St., N.W., WASHINGTON 6, D. C.

CONTENTS

Ontogeny of Physiological Regulations in the Rat
—*E. F. Adolph* (89–137)

Haeckel, Darwin, and Ecology
—*Robert C. Stauffer* (138–144)

The Development of Peat Lands
—*Eville Gorham* (145–166)

New Biological Books

Genetic Variability in Populations
—*C. C. Li* (167–170)

Reviews and Brief Notices (170–216)